A MODEL OF ADULT AND EGG POPULATIONS OF *Anticarsia gemmatalis* Hubner (LEPIDOPTERA: NOCTUIDAE) IN SOYBEAN

By

BEN GREGORY, JR.

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To My Friends

"Any glimpse into the life of an animal
quickens our own and makes it so much
the larger and better ever way."

John Muir, 1880

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Abstract of Dissertation Presented to the Graduate School of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

A MODEL OF ADULT AND EGG POPULATIONS OF Anticarsia gemmatalis Hubner (LEPIDOPTERA: NOCTUIDAE) IN SOYBEAN

By

BEN GREGORY, JR.

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Major Department: Department of Entomology and Nematology

A model of adult and egg populations of the velvetbean caterpillar (*A. gemmatalis*) was constructed and validated. The model mimicked velvetbean caterpillar (VBC) egg densities in a soybean field within 95% confidence intervals of estimated means. Model construction was based on data from nine separate experiments (1980-84) that allowed for an understanding or quantification of the following: adult moth identification, adult behavior in the field, relative and absolute estimates of adult density, female reproductive states, egg identification, egg developmental rates, absolute estimates of egg density, and the impact of various environmental variables on adult and egg dynamics.

Adult density estimates were obtained with a blacklight trap and an unique adult trap-cage. These density estimates were calibrated with a linear regression equation that was used in the model structure to

predict the number of ovipositing females in the field. The capture of adults in the blacklight trap (BLT) coincided with the appearance of eggs in the field, while adult residency in the field appeared to be delayed until an appropriate vapor pressure deficit had been reached in the field. Dissections of adult females revealed that most females were mated and contained large amounts of fat body. Select physical variables were explored with multiple linear regression for their effect on blacklight trap catch but no consistently adequate correlations were uncovered.

Velvetbean caterpillar eggs were shown to be polychromatic during development. These color changes were temperature-dependent and were used to age field collected eggs. Egg densities predicted by the model were more accurate with a variable ovipositional rate as opposed to a constant rate. The variable ovipositional rate was linked to changes in soybean phenology. In model validation, 65% of the model's predicted values fell within 95% confidence intervals of field estimates. Differences between predicted and estimated values were attributed to unpredictable fluctuations in BLT catch and to variation in ovipositional rate between years.

CHAPTER I
INTRODUCTION

Soybean, Glycine max (L.) Merrill, is presently the most important grain legume in the world and is used for food, medicine, and oil (Weiss 1983). Farmers in the United States produce ca. 56% of the world's soybean or ca. 43 million metric tons (FAO 1984). Thirty-seven percent of the soybean production in the United States occurs in the southeast, and this percentage is expected to increase considerably by the year 2000 because of an increasing worldwide demand (Turnipseed et al. 1979). Soybean production in the southeastern United States is plagued by numerous pest problems (e.g., insects, weeds, nematodes, and plant pathogens), and these problems are expected to escalate because of the increasing acreage being devoted to this crop (Turnipseed et al. 1979).

One way to explore alternative strategies for the management of soybean pests is through the utilization of crop/pest models, where the models are mathematical representations (computer simulated) of the interactions between the crop and its principal pest-species (Stimac and O'Neil 1985). Crop/pest models can be used "to simulate the dynamics of a crop and pests in a single field so that decisions can be made regarding pest management and other production practices for that field. The objective of building a crop/pest model is to describe the dynamics of the crop and pests in the context of the environment in which they coexist. The environment includes many factors influencing the growth of the crop and pest populations: weather inputs, such as temperature,

rainfall and solar radiation; biological inputs, such as natural enemies of the pests; and production system inputs, such as irrigation, cultivation, and application of pesticides" (Stimac and O'Neil 1985, pp. 323-324). These factors must be quantified and mathematically described in submodels of the crop, pests, and production tactics.

One of the objectives of a multi-university investigation* was to construct a soybean crop model that could be used to evaluate soybean production strategies under various combinations of stresses (e.g., water or pests). To accomplish this objective, the Soybean Integrated Crop Management (SICM) model was constructed. This model is composed of an aggregate of submodels coupled to a physiologically-based plant-growth model of soybean, and is designed to allow the user to study various management strategies at the field level for different weather, cultural, soil, pathogen, weed, and insect scenarios (Wilkerson et al. 1982, 1983).

One of the SICM submodels represents the population dynamics of velvetbean caterpillar (VBC), Anticarsia gemmatalis Hubner (Lepidoptera: Noctuidae), a major defoliating pest of soybean (Herzog and Todd 1980, Wilkerson et al. in press). In the current version of the VBC submodel, immigration of VBC adults into soybean has been difficult to assess because no data of adult or egg density are available (see Wilkerson et al. 1982). Data on adult density are essential for model initialization, as VBC life stages do not overwinter in soybean and infestation depends on the annual immigration of adults into soybean

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*Investigation entitled The Development of Comprehensive, Unified, Economically, and Environmentally Sound Systems of Integrated Pest Management--funded by the Environmental Protection Agency and the United States Department of Agriculture.

fields (see Herzog and Todd 1980, Wilkerson et al. 1983). Furthermore, egg density data are essential for model construction because the mere presence of adults does not connote the presence of eggs and the resultant defoliating larvae. The absence of VBC immigration data is not surprising because the control recommendations for most pests are designed without consideration for quantitative estimates of pest immigration (see Barfield and O'Neil 1984).

To assess immigration in the current version of the VBC Submodel, adult and egg densities were estimated from larval densities (Stimac,* personal communication). Changes in the density and timing of adult influx resulted in notable differences in soybean yield and grower profit (see Table 1.1). With density varied and timing of influx held constant, profit per hectare varied from $169.21 (low density) to -$214.26 (high density). With influx timing varied and density held constant, profit per hectare varied from $178.43 (late influx) to -$289.63 (early influx). Without VBC (i.e., a simulation control), profit per hectare was $241.61, the highest of all the simulations. Clearly, the need to investigate VBC immigration into soybean was delineated through the use of these simulations.

Present research goals were to (1) investigate the immigration of VBC adults into soybean, (2) explore the interactions between soybean phenology and VBC adults, and (3) quantify adult and egg densities in soybean. These goals were accomplished by the construction of an adult

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*J. L. Stimac, Associate Professor, Department of Entomology and Nematology, University of Florida, Gainesville, FL 32611. Larval densities at time "t" were used to determine egg and adult densities at time "t-1" by calculating the densities of adults and eggs required to produce the known larval densities. Mortality values of adults and eggs were used in these calculations.

Table 1.1. Comparison of soybean yield and profit among various densities and timings of adult velvetbean caterpillar influx, as simulated with the Soybean Integrated Crop Management model (modified from Wilkerson et al. 1982). Soybean was not irrigated in any simulations.

VBC[a] Density	Influx[b] Timing	Yield (Kg/ha)	Profit ($/ha)
Low	Normal	1896.18	169.21
Average	Normal	1493.02	65.70
High	Normal	403.97	-214.26
Average	Early	110.32	-289.63
Average	Normal	1493.02	65.70
Average	Late	1931.86	178.43
None	None	2177.57	241.61

[a]High = +0.5 * Average; Low = -0.5 * Average.

[b]Early was 30 days prior to normal and late was 30 days later than normal.

and egg population model. The objective of this model is to mimic the number of eggs laid by VBC adults in a 1 ha soybean field. To accomplish this objective, experiments were conducted to understand or quantify (1) egg identification, (2) egg developmental rates, (3) estimates of the absolute density of eggs, (4) adult identification, (5) observations of adult behavior in the field, (6) estimates of the relative and absolute densities of adults, (7) categories of female reproductive states, and (8) the impact of various environmental variables (e.g., temperature) on adult and egg dynamics. Experimental methods, results, and discussions are presented in the chapters and appendices that follow.

Chapter II is a general review of soybean ecology, VBC ecology, and VBC/soybean interactions. Chapter III is a study on the field behavior of adult VBC. Chapter IV is a study on sampling for adults, of the relationships between adult density and selected environmental variables, and of the determination of female reproductive categories. In Chapter V, an egg sampling technique and egg density data are presented. In Chapter VI, a model of VBC adult and egg populations is presented, and Chapter VII contains the summary and conclusions.

CHAPTER II
LITERATURE REVIEW

Introduction

Accomplishment of present objectives (see Chapter I) demanded that soybean, velvetbean caterpillar (VBC), and the environment of both be viewed as interacting components of a system. Velvetbean caterpillar use soybean as an adult ovipositional substrate (see Greene et al. 1973), a larval food source (see Moscardi et al. 1981a), and an adult habitat (see Herzog and Todd 1980). Soybean foliage and yield decrease with VBC larval consumption (Strayer 1973), and temperature affects the growth of both species (see Parker and Borthwick 1943, Johnson et al. 1983). Obviously, to view soybean and VBC as components of a system requires an understanding of the ecology of each species. The objective of this chapter is to review briefly the ecology of soybean and VBC, their relevant interactions, and environmental factors that affect both.

Soybean Ecology

Soybean, *Glycine max* (L.) Merrill, became a domesticated species probably in the North China Plains around the 11th century (Hymowitz 1970). The progenitor species apparently was *G. ussuriensis* Regel and Maack (Morse et al. 1949). Polhill and Raven (1981) provide part of the hierarchical classification for soybean as follows:

Order: Rosales

Family: Leguminosae

Subfamily: Papilionoidae

Tribe: Phaseoleae

Subtribe: Glycininae

Introduced into the United States as early as 1804, this legume did not become an important crop in this country until about 1890 (Morse 1927). Soybean currently is distributed worldwide (Weiss 1983).

General Description

Soybean is a summer annual, usually bushy and upright, and 30-122 cm in height (McGregor 1976, Weiss 1983). The main stem has 14-26 nodes; however, the first 2 nodes actually are composed of 2 opposite nodes. Two cotyledons are borne at the first node, whereas the second node bears two primary leaves. All other nodes on the main and lateral stems bear alternate and pinnate trifoliolates on long petioles; however, some multi-foliolate lines do occur (Shibles et al. 1975). Pubescence occurs on most of the above-ground plant surface and may act as a resistance mechanism to insect oviposition or feeding (see Kobayashi and Tamura 1939, Nishijima 1960, Kogan 1975, Turnipseed 1977, Oliveira 1981).

"The root system is extensive, with a tap-root which may exceed 1.5 m in length, giving rise to many lateral branches usually in the 0-30 cm horizon. However, there is considerable variation between cultivars in respect of rate of growth, total amount, spread and degree of penetration of roots. Roots initially elongate faster than above-ground growth, and in the field under normal conditions, roots of rain-growth plants will be twice as long as above-ground plant height at the six-node stage" (Weiss 1983, p. 344). Root nodules occur due to symbiosis with a nitrogen fixing bacterium, *Bradyrhizobium japonicum*

(Buchanan 1980) comb. nov.* (see Weiss 1983). From a study on the partitioning of C14 photosynthate in soybean, Housely et al. (1979) speculate that less carbon is channeled into amino acids of nodulated plants, as opposed to non-nodulated plants. The significance of this channeling is unclear, but perhaps nodulated soybean can channel more carbon into seed formation and plant defense.

Development and Growth

Fehr and Caviness (1977) describe and illustrate the stages of soybean development based on vegetative and reproductive states (Tables 2.1 and 2.2). Soybean is a short-day plant, and reproduction (or flowering) is triggered by photoperiod (Garner and Allard 1930). Temperature and variety can be important in determining the beginning of flowering (van Schaik and Probst 1958, Fehr and Caviness 1977). Flowering occurs over a four to six-week period (Shibles et al. 1975). Flowers are self-pollinated (Shibles et al. 1975, McGregor 1976), but Erickson (1975) demonstrated a significant yield increase in two varieties due to honey-bee, *Apis mellifera* L., pollination. Soybean flowers do produce nectar (Jaycox 1970) and possess most, if not all, of the anatomical adaptations of entomophilious plants (e.g., the nectar guide)(Erickson and Garment 1979).

Soybean exhibits two types of growth habit, determinate and indeterminate. Canopies of these two growth types are distinctly different. The largest leaves of indeterminates occur at the center of the plant, with gradations in size toward each end of the stem. With determinate cultivars, all mature leaves above the middle of the plant

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*Synonym is *Rhizobium japonicum* Buchanan (Jordon 1982).

Table 2.1. Description of soybean vegetative stages (Fehr and Caviness 1977).

Stage	Stage Title	Description
VE	Emergence	Cotyledons above the soil surface.
VC	Cotyledon	Unifoliolate leaves unrolled sufficiently so that leaf edges are not touching.
V1	First-Node	Fully developed leaves at unifoliolate nodes.
V2	Second-Node	Fully developed trifoliolate leaf at node above the unifoliolate nodes.
V3	Third-Node	Three nodes on the main stem with fully developed leaves beginning with the unifoliolate nodes.
V(n)	nth-Node	The number of nodes on the main stem is equal to 'n', beginning with the unifoliate nodes.

Table 2.2. Description of soybean reproductive-stages (Fehr and Caviness 1977).

Stage	Stage Title	Description
R1	Beginning Bloom	One open flower at any node on the main stem.
R2	Full Bloom	Open flower at one of the two uppermost nodes on the main stem with a fully developed leaf.
R3	Beginning Pod	Pod 5 mm long at one of the four uppermost nodes on the main stem with a fully developed leaf.
R4	Full Pod	Pod 2 cm long at one of the four uppermost nodes on the main stem with a fully developed leaf.
R5	Beginning Seed	Seed 3 mm long in a pod at one of the four uppermost nodes on the main stem with a fully developed leaf.
R6	Full Seed	Pod containing a green seed that fills the pod cavity at one of the four uppermost nodes on the main stem with a fully developed leaf.
R7	Beginning Maturity	One normal pod on the main stem that has reached its mature pod color. Mature pod color varies with variety.
R8	Full Maturity	Ninety-five percent of the pods that have reached their mature pod color. Five to ten days of drying weather are required after R8 before the soybeans have less than 15% moisture, and can be harvested.

are approximately the same size, and their resultant canopies are thought to have poorer light-distribution characteristics. Indeterminate cultivars continue to grow vegetatively during flowering, and early pod, and seed development. Flowering begins when these cultivars have reached about half their height and continues as the plant grows taller. For determinate varieties, plants reach full height at flowering and flowers emerge at approximately the same time from all nodes (Fehr et al. 1971, Shibles et al. 1975, Fehr and Caviness 1977).

Fehr and Caviness (1977) provide average and range estimates of soybean development between stages (see Table 2.3). The average number of days for complete development is 125, with a range of 74 to 218. The large range in developmental time results from effects of temperature, variety, photoperiod, and water stress (Doss et al. 1974, Fehr and Caviness 1977). The major factor that influences vegetative growth is temperature. Seedling emergence and leaf development are retarded by low temperatures and enhanced by high temperatures (Fehr and Caviness 1977).

Soybean leaves exhibit Calvin-cycle photosynthesis, but stems and pods also contribute to carbon dioxide uptake (Weiss 1983). Leaf area production begins slowly, then increases rapidly and increases almost linearly during mid-vegetative growth. Maximum leaf-area index (LAI*) values of five to eight can be achieved by late flowering. During seed filling and after flowering, LAI declines progressively by abscission of lower leaves (Shibles et al. 1975).

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*Leaf Area Index (LAI) is "the surface area of leaves per unit surface area of ground" (Lewis 1977, p. 87).

Table 2.3. Average and range of developmental time required for a soybean plant to develop between stages (Fehr and Caviness 1977).

Stage	Average[a] Developmental Time (day)	Range in[b] Developmental Time (day)
0[c] - VE	10	5 - 15
VE - VC	5	3 - 10
VC - V1	5	3 - 10
V1 - V2	5	3 - 10
V2 - V3	5	3 - 8
V3 - V4	5	3 - 8
V4 - V5	5	3 - 8
V5 - V6	3	2 - 5
R1 - R2	0[d], 3	0 - 7
R2 - R3	10	5 - 15
R3 - R4	9	5 - 15
R4 - R5	9	4 - 26
R5 - R6	15	11 - 20
R6 - R7	18	9 - 30
R7 - R8	9	7 - 18

[a] Average total developmental time is 125 days.

[b] Range varies from 74 to 218 days.

[c] 0 = planting

[d] R1 and R2 generally occur simultaneously in determinate varieties. The time interval between R1 and R2 for indeterminate varieties is about three days.

Water Stress

"Soybeans use a lot of water" (Shibles et al. 1975, p. 159). With sufficient water, total water use from beginning bloom to maturity is nearly the equivalent of 95% open-pan evaporation (Peters and Johnson 1960). Water consumption by soybean is determined substantially by leaf area until full ground-cover is achieved. After full ground-cover, evaporative demand is the most influential variable. Leaf area distribution and water supply also affect water consumption. Soybean is water-stressed easily and may be under water stress more frequently and severely than many other plants. Water stress is caused by soil water deficit or high evaporative demand. Even on wet soils, plants can exhibit wilting under high evaporative demand (Shibles et al. 1975).

Susceptibility to Insect Attack

Soybean is susceptible and sensitive to insect attacks for at least three reasons: (1) It is grown in monoculture in large acreages--approximately 25 million hectares were harvested in the United States in 1983 (see FAO 1984). The "plant apparency" of soybean, due to this acreage, makes it potentially highly vulnerable to insect herbivory (see Feeny 1975). (2) As part of a simplified agroecosystem with high-energy input, soybean, like other crops of the Green Revolution,* is highly susceptible to insect attack (see Perelman 1977, Altieri 1983). (3) Soybean may have inadequate defenses against many insects, as man has introduced soybean into the range of these insects. For example, VBC apparently evolved in the Neotropical region (see Buschman et al. 1977) while soybean evolved elsewhere (see Weiss 1983).

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*The Green Revolution is an attempt to solve crop production problems through the development of high-yielding varieties that require high inputs of pesticides, fertilizers, irrigation, and machinery.

Velvetbean Caterpillar Ecology

Anticarsia gemmatalis Hubner was described by Hubner (1816, cited by Ford et al. 1975). Kimball (1965) and Borror et al. (1981) provide part of the hierarchial classification for this insect as follows:

Order:	Lepidoptera
Suborder:	Ditrysia
Superfamily:	Noctuoidea
Family:	Noctuidae
Subfamily:	Erebiinae.

Seven synonyms for *A. gemmatalis* are listed by Schaus (1940). The common name for *A. gemmatalis*, as accepted by the Entomological Society of America, is the velvetbean caterpillar (Sutherland 1978). Severe defoliation of velvetbean (*Stizolobium deeringianum* Bort.) by this insect in the early 1900's resulted in its common name (Chittenden 1905, Watson 1916a).

Distribution

The VBC is a tropical to subtropical species of the Western Hemisphere (Ford et al. 1975) and ranges over much of North and South America, and all of Central America and the West Indies. In North America, the northern limits of the range are slightly above the 45°N parallel, extending into Ontario and Quebec, Canada. In South America, the southern limit of the range appears to be approximately the 35°S parallel, extending to Buenos Aires, Argentina (Ford et al. 1975, Herzog and Todd 1980).

The range of VBC in North America fluctuates temporally due to (1) suspected migration of adults (Watson 1916a), (2) winter mortality of immature stages (Buschman et al. 1981a), and (3) lack of occurrence of immature stages (Ellisor 1942, Buschman et al. 1977, Waddill et al.

1982). Evidence to support migration is either speculative (see Watson 1916a) or indirect (Baust et al. 1981, Buschman et al. 1981a). No intensive studies of adult distribution in the winter exist, nor have direct-evidence studies (e.g., capture, mark, release, recapture) of adult migration been made. The 28°N parallel has been indicated as the northern limit for winter distribution (Buschman et al. 1977), but some reports appear to conflict with this limit. A number of adults were caught in Gainesville, FL, following a freeze that occurred on 21 November 1914 (Watson 1915). Adults were caught again in Gainesville on 29 January 1916 (Watson 1916a) and on 4 March 1932 (Watson 1932) at the 29°38'N parallel, 188 km above the 28°N parallel.

Life Stages

A description of VBC life stages is given by Watson (1916a) as egg, six larval instars, pupa, and adult. The egg is nearly 2 mm in diameter, less than 2 mm in height, prominently ribbed, and flattened on its lower surface (Watson 1916a). Egg coloration varies greatly: white, delicate pink, pale green, cryptic green, orange, reddish brown, transparent, slightly green, and green with red marks (see Watson 1916a, Douglas 1930, Hinds 1930, Ellisor 1942, Greene et al. 1973, Gutierrez and Pulido 1978). Larvae vary greatly in color and markings, particularly after the second instar. Longitudinal lines are usually black, white, yellow, or pink. Background color varies from light yellowish-green to mahogany brown. Length of a sixth instar larva varies from 38 to 48 mm (Watson 1916a).

Pupae are light green for approximately 24 hours, then turn brown. Pupation occurs usually at or below soil surface and in a loose, frail, earthen cell (Watson 1916a, Hinds 1930). Dorsal wing coloration of the adults is highly variable, with color ranging from ashen gray to light

yellowish-brown to reddish brown (Watson 1916a, Kimball 1965, Leppla et al. 1977). Ventral coloration is more consistent, a cinnamon brown with a submarginal row of white spots (Watson 1916a). Sexual dimorphism of adult leg scales allows for accurate and rapid sexual identification. Males have tufts of long setae that are present on the femora of prothoracic legs and the tibiae of metathoracic legs. These long setae are absent on female legs (Anonymous 1974).

Life History

The life history of VBC in the field is discussed by Watson (1916a), Douglas (1930), Hinds (1930), Hinds and Osterberger (1931), Ellisor (1942), Buschman et al. (1977), Gutierrez and Pulido (1978), and Buschman et al. (1981a). Leppla (1976) and Leppla et al. (1977) report the life history under laboratory conditions. Larval development and consumption on different phenological stages of soybean are reported by Reid (1975), Moscardi et al. (1981a), and Olivera (1981). Nickle (1976) gives larval consumption rates on peanut leaves. Moscardi et al. (1981b) and Olivera (1981) report the effect of different soybean phenological stages on VBC oviposition, egg hatch, and adult longevity. Finally, Moscardi et al. (1981c) demonstrate the effects of temperature on oviposition, egg hatch, and adult longevity, and Johnson et al. (1983) present a temperature-dependent developmental model of VBC.

Adult Behavior

Field and laboratory studies have been conducted on adult behavior. In general, the field studies have been qualitative, with little quantification of data. The reverse exists for the laboratory studies. Observations of adults with regard to oviposition, mating, feeding, and flight activity are reported by Watson (1916a), Douglas (1930), Hinds (1930), Greene et al. (1973), and Ferreira and Panizzi (1978). Greene

et al. (1973) present the most detailed observations, but their data were collected over a short, seven-day time period. Johnson et al. (1981) report a behavioral study on the response of VBC to its pheromone. Heath et al. (1983) elucidate the chemical composition of VBC pheromone and the pheromonal effect on male and female behavior. Leppla (1976) and Leppla et al. (1979) indicate the circadian rhythms of locomotion and reproductive behavior of adults in the laboratory. Wales et al. (1985) demonstrate the flight and ovipositional dynamics of adult females during tethered flight.

Host Plants

At least 40 legumes and five non-legumes appear to serve as host plants for larvae of the VBC (Table 2.4). The authenticity of many of the records in Table 2.4 is questionable because they were not accompanied with (1) host scientific name, (2) confirmation of oviposition, (3) verification of complete larval development, (4) verification of larval and host identities, and (5) multiple sightings. Based on these records VBC probably is restricted to leguminous host plants and is therefore either monophagous (see Krieger et al. 1971) or oligophagous (see Slansky 1976).

Velvetbean caterpillars appear to have a marked preference for soybean over other hosts. Douglas (1930) states that neither larvae nor feeding damage was sighted, except on soybean, in fields planted with soybean and the following crops: cotton,* kudzu, cowpea, and velvetbean. Hinds and Osterberger (1931) note a similar preference for soybean grown with velvetbean, cowpea, and other legume crops (names

*Some larvae crawled from completely defoliated soybean to cotton and fed on the cotton. Complete larval-development on the cotton was not assessed.

Table 2.4. Reported host plants[a] of larval velvetbean caterpillar (modified from Moscardi 1979, Herzog and Todd 1980).

Family	Scientific Name	Common Name	Reference
Leguminosae	Aeschynomenes sp.	Joint Vetch	DPI[b]
	Agati grandiflora (L.) Desv.	Gallito Trees	Wolcott (1936)
	Arachis hypogaea L.	Peanut	Anonymous (1928)
	Cajanus cajans (L.) Millsp.	Pigeon Pea	McCord (1974)
	Cajanus indicus Spreng	Pigeon Pea	DPI[b]
	Canavalia gladiata (Sav.)	Sword Bean de Cond.	Ellisor (1942)
	Canavalia maritima Aub.	Horse Bean	Buschman et al. (1977)
	Canavalia rosea Sw.	Canavalia	Tietz (1972)
	Canavalia sp.	---	Watson (1916a), Ellisor (1942), Tietz (1972)
	Cassia fasciculata Michx.	Partridge Pea	Herzog (unpublished)[c]
	Cassia obtusifolia L.	Coffeeweed	Buschman et al. (1977)
	Desmodium floridanum Chapm.	Beggar Lice	Buschman et al. (1977)

Table 2.4 (continued)

Family	Scientific Name	Common Name	Reference
Leguminosae	Dolichos lablab L.	Hyacinth Bean	Buschman et al. (1977)
	Galactia spiciformis	Galactia Torr. and Gray	Buschman et al. (1977)
	Glycine max (L.) Merrill	Soybean	Nickels (1926)
	Indigofera hirsuta L.	Hairy Indigo	Buschman et al. (1977)
	Lespedeza sp.	---	USDA (1954a)
	Medicago sativa L.	Alfalfa	Ellisor and Graham (1937)
	Melilotus alba Desr. in Lam.	White Sweet Clover	Waddill (1981)
	Pachyrhizus erosus (L.) Urban	Yam Bean	Buschman et al. (1977)
	Phaseolus calcaratus Roxb.	Frijolito Rojo	Gutierrez and Pulido (1978)
	Phaseolus lathyroides L.	Wild Bean	Buschman et al. (1977)
	Phaseolus limensis Macf.	Lima Bean	Ford et al. (1975)
	Phaseolus max[e]	---	Wolcott (1936)
	Phaseolus semierectus[e]	---	Tietz (1972)
	Phaseolus speciosus H.B.K.	Sweet Pea Vine	Buschman et al. (1977)

Table 2.4 (continued)

Family	Scientific Name	Common Name	Reference
Leguminosae	Phaseolus vulgaris var.	Bush Bean humilis Alef.	Ford et al. (1975)
	Pisum sativum L.	English Pea	DPI[b]
	Pisum sp.	Field Pea	DPI[b]
	Pueraria lobata Willd.	Kudzu	Buschman et al. (1977)
	Pueraria phaseoloides (Roxb)	Tropical Kudzu Benth	Ford et al. (1975)
	Pueraria thumbergiana (Siebold and Zucc.) Benth	Kudzu Vine	Watson (1916a)
	Rhynchosia minima L.	Least Rhynchosia	Buschman et al. (1977)
	Robinia pseudoacacia L.	Black Locust	Ellisor (1942)
	Sesbania emerus (Aubl.) Britton and Wilson	Long Pod	DPI[b]
	Sesbania exaltata (Raf.) V.L. Cory	Sesbania	Tietz (1972)
	Sesbania macrocarpa Muhlenb. ex Raf.	Coffee Weed	Hinds and Osterberger (1931)

Table 2.4 (continued)

Family	Scientific Name	Common Name	Reference
Leguminosae	*Stizolobium deeringianum* Bort.	Velvetbean	Chittenden (1905)
	Tephrosia sp.	---	USDA (1954b)
	Vigna luteola Jacq.	Vigna	Buschman et al. (1977)
	Vigna repens (L.) Kuntze	Cowpea	DPI[b]
	Vigna sinensis (L.) Endl.	Cowpea	Hinds and Osterberger (1931)
Begoniaceae	*Begonia* sp.	Begonia	DPI[b]
Gramineae	*Oryza sativa* L.	Rice	Tarrago et al. (1977)
	Triticum sp.	Wheat	Wille (1939)
Malvaceae	*Gossypium herbaceum* L.	Cotton	Douglas (1930)
	Hibiscus esculentus L.	Okra	Todd (unpublished)[d]

Table 2.4 (continued)

[a]The authenticity of many of these records is questionable because they were not accompanied with (1) host scientific name, (2) confirmation of oviposition, (3) verification of complete larval development, (4) verification of larval and host identities, and (5) multiple sightings.

[b]Host records on file at Florida Department of Agriculture and Consumer Services, Division of Plant Industry (DPI), Gainesville, FL 32611.

[c]D. C. Herzog, Professor, Entomology and Nematology Department, University of Florida, Agriculture and Education Center, Quincy, FL 32351.

[d]J. W. Todd, Assoc. Professor, Department of Entomology, University of Georgia, Georgia Coastal Plain Experiment Station, Tifton, GA 31794.

[e]Author unknown.

not provided). Ellisor and Graham (1937, p. 278) state that "moths select soybeans in preference to velvet beans for oviposition, even when the two crops are grown in adjacent fields." Ellisor (1942) reports soybean is preferred to alfalfa, cowpea, peanut, and velvetbean. Oddly, no studies of VBC and its hosts, except for soybean (see Moscardi et al. 1981a, 1981b) and peanut (see Nickle 1976), have been conducted to assess complete larval development, and adult eclosion.

Natural Enemies

An extensive review and discussion of the parasitoids, predators, and pathogens of VBC is provided by Moscardi (1979). Two striking generalizations about VBC natural enemies that emerge from a synthesis of Moscardi's review are (1) the predators and parasites are generalists and (2) the pathogens are highly specific. O'Neil (1984) reports that predators are unable to control VBC populations because the predators are generalists and do not search sufficient leaf area. At the present time, pathogens appear to be the best natural enemy for controlling VBC populations (see Kish and Allen 1978).

Sampling and Economic Thresholds

Sequential sampling and economic thresholds for management of VBC larvae in soybean are presented by Strayer (1973). Estimates of the relative and absolute densities of larvae in soybean are presented by Luna (1979). Linker (1980) provides sampling procedures for larvae in peanuts and soybeans, and presents an analysis of seasonal abundance. Techniques and methodologies for sampling of all VBC stages are reviewed and discussed by Herzog and Todd (1980).

Models

At least six models of VBC dynamics in soybean are reported. Menke (1973) and Menke and Greene (1976) present a stochastic simulation model

in which VBC dynamics and soybean defoliation are examined. Kish and Allen (1978) present a model predicting the incidence of Nomuraea rileyi (Farlow) Samson on VBC larvae. Luna (1979) reports an economic threshold model for chemical control of VBC larvae on soybean. O'Neil (1984) presents a model of predation on larvae. Predator and VBC densities, soybean leaf-area, and predator searching-behavior are incorporated into O'Neil's model. The Soybean Integrated Crop Management (SICM) model is a soybean plant-growth model that is coupled to multiple stress submodels (e.g., an insect-pest submodel). One of these submodels represents the population dynamics of the velvetbean caterpillar (Wilkerson et al. 1983). Wilkerson et al. (in press) present a temperature dependent VBC dynamics model.

Velvetbean Caterpillar as a Soybean Pest

Velvetbean caterpillars are a chronic and primary pest of soybean for many reasons. Adults are highly mobile, exhibit early reproduction, and have a very high reproductive rate, while larvae develop rapidly and exhibit high survival. In short, VBC appears to be an r-strategist* (see MacArthur and Wilson 1967). Adults are caught as far north as Canada (Watson 1916a) and on oil-rig platforms in the Gulf of Mexico (Baust et al. 1981). Further, adults exhibit a low wing-loading ratio** that may require little energy for flight and may be an adaptation for flying long distances in search of host plants (Angelo and Slansky 1984); larvae utilize host plants that are widely dispersed and

*The crucial evidence needed for r- and K-selection is whether an organism allocates a greater proportion of its resources to reproductive activities (r-strategist) than another related organism (K-strategist) under any and all density-dependent and density-independent mortality conditions.

**Wing loading ratio is body weight/wing area.

ephemeral (see Herzog and Todd 1980), so adults must be able to fly between hosts. Mated females exhibit early reproduction, laying 50% of their eggs within four to nine days after emergence, and with oviposition steadily declining thereafter (Moscardi et al. 1981c). Total mean oviposition, for females reared as larvae on soybean, can be as high as ca. 963 eggs/female, with an extremely high net reproductive rate of ca. 365 (Moscardi et al. 1981b). In conjunction with this high reproductive rate, the mean developmental time from egg hatch to adult eclosion is ca. 22 days (Moscardi et al. 1981a). Finally, immature VBC stages exhibit high survival, except for larval mortality during late soybean growth from the pathogen, N. rileyi (Kish and Allen 1978, Elvin 1983, O'Neil 1984).

Velvetbean Caterpillar/Soybean Interactions

The VBC is believed to overwinter in southern Florida, the West Indies, Central America, and much of South America. This pest is hypothesized to migrate each year from overwintering areas into the southern United States (Watson 1916a, Herzog and Todd 1980, Buschman et al. 1981a). The temporal occurrence of immigration is unknown, as no direct evidence exists (Buschman et al. 1981a), but moths invade soybean fields in northern Florida from May to July (Greene 1976). Following colonization, larvae reach peak densities in August or September, or occasionally in early October (see Greene 1976, Linker 1980). As soybean senesces, usually in mid to late October, larval populations decline rapidly and VBC adults move to different hosts, both cultivated and wild (Ellisor 1942, Greene 1976, and Buschman et al. 1981a). Larvae and pupae apparently are incapable of overwintering in soybean fields, so infestation of soybean the next year begins with adult immigration (Watson 1916a, Buschman et al. 1981a).

Soybean and VBC interact in several ways: (1) oviposition by moths, (2) foliage consumption by larvae, (3) nutritional quality of plants, and (4) canopy dynamics of the plants. Soybean serves as an ovipositional substrate (Greene et al. 1973), and differences in infestation levels on some varieties may be due to an ovipositional preference (see Genung and Green 1962). Soybean varieties and phenological stages vary nutritionally (see Hammond et al. 1951, Henderson and Kamprath 1970, Hanway and Weber 1971), and this variation significantly affects VBC development, consumption, survivorship, and reproduction (Moscardi et al. 1981a, Moscardi et al. 1981b, Reid 1975, Oliveira 1981). Also, as larvae develop, their consumption rate (cm^2/day) increases: instar 2 = 0.31; instar 3 = 1.47; instar 4 = 3.94; instar 5 = 8.11; and instar 6 = 14.39 (Reid 1975).

The dynamics of the soybean canopy have an enormous effect on two aspects of VBC dynamics: (1) adult colonization and (2) larval mortality. Colonization by adults may be related to changes in soybean canopy (see Chapter IV). Canopy dynamics affect larval mortality in four ways. First, canopy closure establishes favorable microclimatic changes that can lead to an epizootic of Nomuraea rileyi (Farlow) Samson, an entomopathogenic fungus (Kish and Allen 1978). Second, mortality rates of immature VBC that have fallen to the ground are significantly higher before the canopy closes due to high soil surface temperature (Elvin 1983). Third, canopy leaf area is a key element in the predator/prey dynamics of VBC larvae. Leaf-area increase provides a spatial escape for VBC larvae (O'Neil 1984). Fourth, female moths appear to oviposit on the lowest two-thirds of the plant and small larvae are apparently distributed in the bottom third of the canopy (see Ferreira and Panizzi 1978). Mortality of eggs and small larvae may

decrease significantly after canopy closure because closed canopies are darker than unclosed canopies and predators may not be able to see as well in a closed canopy.

The completion of the present review of the ecology of soybean and VBC, and their interactions, sets the stage for presentation of the chapters that follow. In the next chapter (Chapter III), a description of the behavioral ecology of adult VBC within soybean is presented. Observations of adult behavior in the field were necessary for the design and implementation of the experiments presented in the chapters that follow Chapter III.

CHAPTER III
BEHAVIORAL ECOLOGY OF ADULT VELVETBEAN CATERPILLAR

Introduction

Ethology, the study of behavior, has been slow to emerge as a scientific discipline (Kennedy 1972, McFarland 1976). This slow emergence seems odd, particularly with respect to pests, because pest management mandates an understanding of pest behavior (Kennedy 1972, Lloyd 1981, Gould 1984, Lockwood et al. 1984). Ignorance of the behavioral ecology of pests has led to a poor understanding of population dynamics and management (see Kennedy 1972, Stimac 1981, Burk and Caulkins 1983, Barfield and O'Neil 1984).

Insect behavioral data, particularly for pests, is limited (Nielsen 1958, Matthews and Matthews 1978). Not surprisingly, information on the behavioral ecology of adult velvetbean caterpillar (VBC), a major pest of soybean in the Gulf Coast area of the United States, is sparse (see Greene et al. 1973, Herzog and Todd 1980). The present study on the behavioral ecology of adult VBC was initiated as part of a project to explore the movement of adults into soybean. To examine this movement quantitatively, a mathematical relationship needed to be established between adult and egg densities in a soybean field (see Chapter VI). To obtain estimates of adult and egg densities (see Chapters IV and V), and to establish a relationship between these estimates, a number of questions about adult behavior in the field had to be resolved: (1) Did flight activity vary through time? (2) Did ovipositional occurrence and frequency vary through time? (3) What environmental factors affected

flight activity and oviposition? and (4) What environmental factors affected the movement of adults in and out of soybean? In addressing these questions, additional behavioral observations were recorded.

Literature Review

General Activity

Circadian rhythms of locomotion for colonized adults have been determined with a vibration-sensitive actograph (Leppla 1976). Males and pairs were diurnal predominately during the first 6 days after emergence and nocturnal from the sixth day until death. Females became nocturnal within 48 h of emergence. The general activity of adults in all categories (i.e., isolated sexes and pairs) was age dependent; most activity occurred in the first week after emergence. For paired adults, 74% of all activity was expressed during the first week.

Flight in the Laboratory

Circadian rhythms of flight frequency for colonized adults were determined with an actograph system (Leppla et al. 1979). Flight activity, monitored for 18 days, was exceptionally erratic. Nocturnal and diurnal flights were common during the first six days after emergence for isolated sexes and pairs. Following the sixth day, flights were nocturnal predominately. No significant differences in flight activity were noted among males, females, or pairs, but pairs exhibited the least activity and isolated females exhibited the most activity. Flight activity for all categories decreased with age.

A pivot-stick actograph was used to examine tethered flight of VBC adults (Wales et al. 1985). No significant differences were detected with regard to mean flight frequency (number of flights) or mean flight duration (time of flight) among all seven comparisons of colony versus wild adults and mated versus unmated adults. For mated and unmated

colony females, mean daily flight frequencies were erratic, but relatively few flights were made in early adult life. No obvious patterns in the hourly distributions of flight frequency for colony or wild females, mated or unmated, were detected. For mated and unmated colony females, mean daily flight durations were erratic, but relatively short flight times were displayed in the second through fourth days. No obvious patterns in the hourly distributions of flight duration for colony or wild females, mated or unmated, were detected.

Flight in the Field

Flight activity in the field can be partitioned into three categories: (1) migratory, (2) movement among various hosts, and (3) within field. Migration of adults is reviewed in Chapter II, and movement among hosts is discussed in Chapter IV where relevant adult-density data are presented. Reports of within-field flight activity (i.e., daily flight activity) will be reviewed in this chapter.

Watson (1915, 1916a, 1916b), the first to report on flight activity of VBC, made several observations in velvetbean, *Stizolobium deeringianum* Bort.

> Although apparently capable of prolonged journeys, the moths as observed in the field, do not ordinarily take long flights. They hang about the velvet bean plants closely, coming out for short flights about sunset. If disturbed, they dart away rapidly but usually fly only a few yards and do not rise high above the vines. (Watson 1915, p. 59)

> Dusk is the period of greatest activity of the moths. During the day they lie hidden under the leaves of the host plants. If disturbed they fly a short distance only. (Watson 1916a, p. 525)

> The moths fly mostly toward sunset, but fly up at any time during the day if the vines are disturbed as by one walking through them. They do not rise high into the air but keep close to the ground and where the shade of the vines is dense. (Watson 1916b, p. 11)

Douglas (1930) indicated that adults were night-flying moths, were inactive in soybean during the day and, if disturbed, exhibited a very swift flight. Ellisor (1942, p. 18) noted:

> The moths are inactive in the day, usually resting on the ground or close to the ground on leaves or other debris, and when disturbed make darting flights for short distances and again become inactive. Late in the afternoon they become active and can be seen darting in and out of the plants.

The most detailed observations of flight were reported by Greene et al. (1973). Moths were observed with a flashlight and a propane lantern in a 1.83 x 1.83 x 3.66 m screen cage placed over soybean plants in a field. "Observation of moths in daylight showed undirected flight behavior. Disturbed moths flew into the cage walls, hit leaves and other objects, and flew in undirected, sharp, angled patterns, similar to the observations by Ellisor (1942). At sunset, moth activity in the field was minor, but 30 min post-sunset, moth movement became directed, slower, and much more controlled. Moths did not fly into the cage walls; they would fly to the wall and light upon it; they would fly to a leaf, flutter, and settle upon it, and they were observed not to bump into objects. Moths on the cage walls at sundown moved to the plants and by ca. 1½ h postsundown few were left on the cage walls" (Greene et al. 1973, p. 1113).

Another report of flight activity in soybean was made by Gutierrez and Pulido (1978). They reported that moths were fast fliers and flew regularly during the night. During the day, moths remained on the soil surface near the soybean plants or on the middle part of the plants. Johnson et al. (1981) reported on the flight of colony males under natural photoperiod in screenwire cages in a greenhouse; females were present but were unable to fly. "Males became active ca. 45 min after

sunset. This activity was characterized by apparently indiscriminate flight around the cage, followed by walking on the sides of the cage, and rapid fluttering of wings" (Johnson et al. 1981, p. 529).

Mating

Watson (1915, p. 60) stated that, "mating undoubtedly takes place at night." Watson (1916a, p. 525) furthered his observations when "a single pair was observed mating in the cages [sic]. This occurred about dusk. They remained *in coitu* only a few seconds."

The first detailed observations of mating behavior were published by Greene et al. (1973). Observations were made during seven consecutive scotophase periods inside a 1.83 x 1.83 x 3.66 m screen cage placed over soybean. Male activity was observed when a female, "with her moving wings outstretched horizontally" (Greene et al. 1973, p. 1113), pointed her abdominal tip dorsally (or ventrally as in one observation). Males, usually two to five, were attracted from .61-1.83 m. A mating pheromone was postulated.

Greene et al. (1973) noted additionally that mating activity consisted of five stages: pheromone release, male response, mounting by the male, sperm transfer, and separation. Males flew in an upwind zigzag pattern to locate a female. Females were approached from behind, stroked vigorously with the male's antennae, and mounted dorsally for 1-10 sec ($\bar{x}$ = 5 sec). Males then rotated 180° toward the rear of the female, so that their heads pointed in opposite directions. The legs of both adults were on a leaf surface, and females always faced skyward. Adults remained opposite to each other for the remainder of the copulatory period, were docile if disturbed, and moved very little.

"The majority of the copulations began within 2 h postsunset and considerably fewer after 10 PM. The time spent in copulation ranged

from 42 min to over 4 h and averaged 2 h 31 min." (Greene et al. 1973, p. 1114). Copulations were observed on the cage wall, on the plants, and in the field outside of the cage. Under natural field conditions, mating occurred within the plant canopy, with both sexes grasping stems or leaves. At the completion of copulation, the adults separated. Usually the female walked a very short distance, remained on the same plant leaf for a few minutes, and then flew away. Male activity after separation was not described.

During a ten hour scotophase period in the laboratory, Leppla (1976) watched 20-50 pairs of adults in three plexiglass cages over an 18-day period. No adults "called" or mated during their first day. Mating peaked during the 2nd and 3rd day and declined steadily until it stopped on the 16th day; mating activity was age-dependent. Mating occurred at all hours of scotophase, with 19% occurring in the first 5 hours and 81% occurring in the second 5 hours. Mated females contained an average of 1.7 spermatophores per female, with a range of 1-6 spermatophores. Males did not mate more than twice. "Typically, a male flew to the female, engaged in the well-known lepidopteran 'courtship dance,' approached the female from behind, moved forward to a parallel position, mounted dorsally, clasped the genitalia of the female, and swung down to face the opposite direction" (Leppla 1976, p. 47).

Johnson et al. (1981) confirmed the presence of a female sex pheromone with behavioral observations and field bioassays. Colony adults, observed in cages in a greenhouse, became active ca. 45 min after sunset, but mating was not noted until ca. 2 h after dark. The courtship sequence was initialized by a female with wing fanning and dorsal elevation of the abdominal tip. The male response consisted of flying in a zigzag path toward the female, hovering near the female

(usually with claspers extended), and landing or flying away. In the field bioassay, male attractiveness to three females in a trap commenced ca. 1 h after sunset and remained fairly uniform throughout the night. Pheromone, extracted from females 4 h and 6 h after sunset, was more attractive to males than pheromone extracted 9 h and 6 h before dark, at sunset, or 2 h and 9 h after sunset. A significant decrease in male capture was noted with increasing age of females. Also, mated females were less attractive to males. The female sex-pheromone was identified as a blend of (Z,Z,Z)-3,6,9-eicosatriene and (Z,Z,Z)-3,6,9-heneicosatriene in a blended ratio of ca 5:3, respectively (Heath et al. 1983). Synthesized pheromone elicited responses by adult males equivalent to those elicited by females in both laboratory bioassays and field-trapping experiments (Heath et al. 1983).

Oviposition

Early reports of oviposition were not quantified. Watson (1916a) noted most eggs were laid singly on the bottom leaf-surface of velvetbean, but some were laid on the upper leaf-surface, petiole, and stem. He also reported oviposition on the tender shoots, the underside of the leaves (Watson 1915), mostly on the bottom of younger leaves (Watson 1916b), and mostly on the bottom of mature leaves (Watson 1916c). Watson apparently was confused as to where the majority of eggs were laid. Watson (1921, p. 2) further reported that, "the moths are shade-loving creatures and collect under the vines in the densest shade and there lay their eggs."

Douglas (1930) indicated that eggs were deposited singly on the underside of soybean leaflets and sometimes on the upper leaflet surface. Females often laid one egg per plant, sometimes several. Hinds (1930) reported that eggs were deposited singly on soybean,

scattered about the plant and found on leaves and stems. On leaves, the midrib was preferred because the pilosity was heaviest. Oviposition was observed by Hinds (1930) at dusk and assumed to continue into the night. Observations by Ellisor (1942) indicated the following: (1) oviposition on soybean began in late afternoon and extended through the night, (2) eggs were laid singly and many eggs were laid on each plant, (3) eggs were found on the stems, seed pods, and leaves, and (4) eggs were found often on the midrib and veins of a leaflet underside.

The only detailed observations of oviposition have been presented by Greene et al. (1973). Wild adults in soybean were observed in a 1.83 x 1.83 x 3.66 m cage during scotophase over a seven-day period. Observations started at sunset (ca. 2000) and stopped at 0300, except for the first night when observations stopped at 0800. Females laid eggs singly, but two or three eggs were laid occasionally at a given site with the eggs ca. 1 cm apart. Females fluttered quickly between ovipositional sites and deposited an egg in 2-60 sec. Frequently, females exhibited ovipositional behavior but no eggs were laid. Eggs were deposited on stems, pods, and leaf bottoms.

"Oviposition was closely observed several times and consisted of the moth first clasping part of the plant with her feet, then arching the tip of her abdomen ventrally. When the plant surface was touched by her abdomen, it expanded; the conjunctiva anterior of her ovipositor became visible, and an egg was deposited. The egg was usually placed between the plant hairs close to the surface, and adhered tightly to the plant. Rain or dew did not remove the eggs, and they were nearly impossible to remove from the leaf with a camel's hair brush" (Greene et al. 1973, p. 1115).

Oviposition occurred throughout scotophase but was most common from 0.5 h after sunset until 0200. A peak in egg laying occurred 2-4 h after sunset. Temperature, humidity, and dew were reported to affect ovipositional activity. Oviposition increased as temperature decreased and humidity increased. Also, oviposition seemed to decrease as dew accumulated, except for the first night. Dew formed from 2200 to 2400 (Greene et al. 1973).

With 20 pairs of colony adults in each of three cages, Leppla (1976) found that egg deposition did not occur during the first 3 days after emergence, peaked on day 5, and declined from day 6 until day 18 when oviposition stopped. Relative humidity (RH) had a critical effect on colony performance. A RH of 85 ± 5%, at least during scotophase, was required for adequate mating. Without adequate conditions for mating, few viable eggs were produced. The placement and vertical distribution of VBC eggs on soybean (cultivar UFV-1) were reported by Ferreira and Panizzi (1978). Eggs were found mainly on the lower two-thirds of plants and most were on pods (59%), some on stems (37%), and a few on leaves (4%).

Moscardi et al. (1981c) investigated the effects of temperature on oviposition, egg hatch, and adult longevity, under constant and variable temperatures. Mean total oviposition was highest at 26.7°C (842.2 ± 26.1 eggs) and steadily decreased in either direction from 26.7°C to the lowest mean at 32.2°C (310.0 ± 14.7 eggs). At temperatures < 18.2°C or > 32.2°C, adult survival and reproductive capacity were retarded significantly. Mean percent egg hatch was (1) highest at 26.7°C, (2) not significantly different for 26.7, 29.4, or 32.2°C, and (3) lowest at 21.1°C. Mean longevity for mated females was longest at 21.1°C (24.8 ± 1.0 days) and steadily decreased to the shortest longevity at 32.2°C

(11.2 ± 0.6 days). At 26.7°C unmated females lived longer (22.8 ± 0.8 days) than mated females (18.0 ± 1.0 days). As temperature increased from 21.1 to 32.2°C, mated females laid the majority of their eggs at progressively earlier ages. At all temperatures, 50% of all oviposition occurred within four to nine days after emergence and steadily declined thereafter.

Females reared from larvae maintained on different soybean phenological stages exhibited variation in mean total oviposition, mean percent egg hatch, mean longevity and R_o (Moscardi et al. 1981b). "Mean oviposition-rates ranged from 963.4 to 515.0 eggs/female when larvae fed on early vegetative and senescent leaves, respectively. Average daily-oviposition peaked ca. 4 days after adult emergence, decreased sharply to day 10, and remained at a low level until adult mortality. Mean daily egg-hatch decreased with female age, but female longevity was not affected significantly" (Moscardi et al. 1981b, p. 113).

Using a pivoted-stick actograph, Wales (1983) confirmed that mated females lay most of their eggs early in life. Unmated females delayed oviposition until very late in life. The hourly distribution for lab mated and wild mated females, ages one to nine days old, indicated that most eggs were laid in the first four hours of scotophase, but that oviposition occurred all night.

Feeding

Not much is known about adult feeding in the field. Hinds (1930) reported adults fed on the nectar of a *Crotalaria* sp. Greene et al. (1973, p. 1115) observed feeding during all hours of scotophase, "with peak activity from sundown to after 12:00 midnight [sic]." Primarily females, but also some males, fed on crushed grapes from sunset until 0230 when observations stopped. Adults fed at the seed heads of

bahiagrass, Paspalum notatum Flugge, throughout scotophase but most abundantly at sunset. The food source on the bahiagrass seed heads was not determined. Moths were observed to feed on dew droplets on soybean and on water in a cup. The chemical content of the dew and water was not determined.

Various honey solutions have been used for adult food in numerous laboratory studies (see Leppla 1976, Leppla et al. 1979, Johnson et al. 1981, Moscardi et al. 1981b, Moscardi et al. 1981c, Oliveira 1981, Wales 1983). The effect of variation in adult diet on oviposition and longevity was explored by Wales (1983). "Moths fed 5% or 10% honey solution had mean longevities of 19.6 and 16.4 days and mean fecundities of 846.1 and 866.2 eggs/female, respectively. Water-fed females lived 9.3 days and produced 212.7 eggs, and unfed females lived 5.7 days and produced 41.6 eggs/female" (Wales 1983, p. ix).

Predators

Little is known about predators of adult VBC. Watson (1915, 1916c) reported dragonflies as predators but listed no common or scientific names. Neal (1974) reported two predatory species, the green jacket dragonfly, Erythemis simplicicollis (Say), and the striped earwig, Labidura riparia (Pallas).

Research Goals

The present study on the behavioral ecology of adult VBC was initiated as part of a project to explore the movement of adult VBC into a soybean field (review pp. 27-28). To examine this movement, a mathematical relationship had to be established between adult and egg densities in a soybean field (see Chapter VI). To obtain estimates of adult and egg densities (see Chapters IV and V), and to establish a relationship between these estimates, a number of questions about adult

behavior in the field had to be resolved: (1) Did flight activity vary through time? (2) Did oviposition occurrence and frequency vary through time? (3) What environmental factors affected flight activity and oviposition? and (4) What environmental factors affected the movement of adults in and out of soybean? In addressing these questions, additional behavioral observations were recorded and are reported below.

Materials and Methods

From 1980-1982,* field observations were conducted at the University of Florida's Green Acres Research Farm, located 22.5 km west of Gainesville, FL (Alachua County). This farm covers ca. 93 ha, and consists of crop fields, fallow fields, and wooded areas. The principal observation site was a 1 ha soybean field (cv. Bragg), but observations were made also at other sites on the farm. Agronomic practices and soybean phenological stages of each soybean field in all three years are listed in Appendix A.

All behavioral observations were made by remaining stationary or walking slowly, and were recorded verbally on a hand-held Panasonic® Microcassette™ Recorder, Model RN-001D. The time of each observation was recorded to the nearest minute. A six-volt Everready® Freedom Light™ (i.e., a head lamp) was used for nocturnal observations; the lighting fixture was covered with a section of Ziptone color sheet, Vermillion Hue #2545. Adult VBC were sexed with leg-scale morphological differences (see Anonymous 1974 and Appendix B), but were not aged. Another moth, *Mocis latipes* Guenee (Lepidoptera: Noctuidae),

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*During the summer of 1983, a few records of adult feeding and spider predation were obtained at various localities. These records are considered ancillary to the text of this chapter but were added where appropriate and with the necessary detail.

occurred at the study site and looked similar to VBC. Differences between adults of these two species are discussed in Appendix B.

Temperature and humidity were monitored continuously with a hygrothermograph (Weather Measure Corporation Model No. H311). Also, temperature was monitored hourly with an Esterline Angus[R] PD2064 Microprocessor. Rainfall was recorded continuously by a Universal Recording Rain Gage (12" chart with dual springs, Belfort Instrument Co.). Sunset and sunrise times were obtained from Oliver* (personal communication). Phase and temporal occurrence of the moon were obtained from the Astronomical Almanac (Smith and Smith 1981, and Vohden and Smith 1982) and were noted with visual observation in the field. In 1981 and 1982, wind speed was recorded at 15 min intervals with a gill, 3-cup, anemometer (Model 12102, R. M. Young Co.). In 1981, wind direction was recorded at 15 min intervals with a gill microvane (Model 12302, R. M. Young Co.).

Quantitative Technique

The temporal occurrence and frequency of several adult activities (oviposition, mating, and feeding) during scotophase were examined quantitatively. Scotophase was partitioned into hourly increments after sunset, with the hours numbered consecutively from 1 (sunset) to 12 (sunrise). For an activity on a particular night, the amount of observation time and the number of observations were segregated according to their hour of occurrence. Observations were weighted with respect to observation time to correct for a time bias (i.e., the number of observations were divided by the amount of observation time). No

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*J. P. Oliver, Associate Professor of Astronomy, Department of Astronomy, University of Florida, Gainesville, FL 32611.

significant differences occurred between years according to the Kruskal-Wallis Test ($\alpha = .05$). Therefore, weighted observations from different years, months, and nights were grouped by hour of occurrence. The sample mean of the weighted observations of each hour was calculated. These sample means were normalized, multiplied by 100 to yield percentages, and plotted against their respective hour.

Sample means were normalized by totaling the 12 hourly sample means and dividing each sample mean by the total. Normalization of the sample means allowed for proportionality among the means. Percent normalized sample means were used for ease of discussion, as opposed to the use of normalized sample means. The standard error of each sample mean was determined, normalized and multiplied by 100. A detailed explanation of the quantitative technique and the raw data are presented in Appendix C.

Assumptions

To analyze the behavioral observations quantitatively, several assumptions were made: (1) an activity had an equal chance of being observed whether I was stationary or walking, (2) adult age did not affect the temporal or spatial occurrence of adult activities (i.e., observed adults were not aged), and (3) the temporal length of scotophase (sunset to sunrise) was the same for all nights.

Results and Discussion

Approximately 355 h were spent observing adult behavior (Table 3.1). The majority of the time (90%) was spent in the field during July, August, and September, and more time occurred during photophase (201 h and 19 min) than during scotophase (153 h and 13 min).

The first adult sightings in 1981 and 1982 occurred during photophase on 3 August and 19 July, respectively. In both years, the first adults were found in areas of the field where the canopy was

Table 3.1. Amount of time dedicated to behavioral observation of adult velvetbean caterpillar in a 1 ha soybean field at the Green Acres Research Farm, Alachua County, FL, from 1980-82.

Month	Scotophase[a] Observation Time (min)				Photophase[b] Observation Time (min)				Total Observation Time (min)
	1980[c]	1981	1982	Total	1980[c]	1981	1982	Total	
June	0	180	359	539	0	90	630	720	1259
July	0	609	1080	1689	0	876	3481	4357	6046
Aug.	180	2159	1158	3497	0	2489	1735	4224	7721
Sept.	0	1717	1401	3118	10	335	1894	2239	5357
Oct.	0	0	350	350	0	30	509	539	889
	Total (min)			9193				12079	21272
	Total (hr/min)			153/13				201/19	354/32

[a]Scotophase was sunset to sunrise.

[b]Photophase was sunrise to sunset.

[c]In 1980, most of the observation times were not recorded.

almost or completely closed. The initial occurrence of adults in the field may be related to microclimatic differences in moisture (see Chapter IV). During the field season, adults were not observed in areas of the field where the canopy was open. Movement of moths out of the field in September and October coincided with the senescing of the soybean and movement into stands of wild hairy indigo (*Indigofera hirsuta* L.). During photophase, moths demonstrated a definite preference for residing in the field, as opposed to the edge of the field. Occasionally, adults were found at the field edge in thick clumps of grass or weeds but, regardless of the location, moths were found always on the ground or close to the ground on plants or dead plant-matter. Areas of high moisture (see Chapter IV), low light, and negligible wind appeared to be preferred. Moths were not observed in areas that were opened and exposed to sunlight and wind.

Flight Activity

Flight activity was assessed qualitatively with visual observations. When approached (or flushed) during photophase, adults flew ca. 1-10 m, landed on the ground or on low vegetation, and became immobile. Flight speed and pattern varied from slow to fast and flutter-like to darting, respectively. Flight direction was highly variable. Adults flew between rows, across rows, within the canopy, over the canopy, and demonstrated numerous combinations of these directions. Flight was controlled, and moths did not hit leaves or other objects, contrary to the report of Greene et al. (1973). Aside from flushed adults, flight activity during the day was very uncommon but consisted of flight just above the canopy and flight while feeding. See the section below entitled "Feeding" for a discussion of in-flight feeding during the day. With regard to flight just above the canopy,

one or more moths were observed in this activity on four different days. Flight activity occurred within ca. 15 min of sunset and flight distance varied from ca. 1 m to greater than 100 m; after 100 m adults were too difficult to observe. Flight speed and pattern usually were fast and darting, respectively.

During scotophase, flight activity was highly evident and temporally variable. During the first ca. 15 min after sunset, flight activity usually was negligible with ca. 0 to 20 flights. Between ca. 15 and 30 min after sunset, flight activity appeared to double but, on one night in September of 1980 (no record of date), several hundred adults were observed flying at this time. From ca. .5 to 2.5 h after sunset, flight activity peaked and then slowly decreased from ca. 2.5 to 4.5 h after sunset. Between 4.5 h post-sunset and sunrise, flight activity was minimal and decreased steadily to zero flights at sunrise.

Flight was utilized for oviposition, mating, feeding and, presumably, general dispersal. Flight distance varied from ca. .01 m to greater than 100 m, but after 100 m flying adults were not observable. Flight speed and pattern varied from slow to fast and flutter-like to darting, respectively.

The most striking flight activity consisted of ca. 3 to 10 adults of unknown sex that appeared to fly in formation. Five of these formations were observed. Each occupied ca. 1 m^3 in volume, occurred at or below the top of the soybean canopy, moved in one direction across or between rows, and varied in speed from moderately fast to fast. Flight paths of individual moths were highly convoluted. Formations looked like a writhing group of moths, lasted from ca. 7 to 30 sec and covered from ca. .03 to 10 m. The nature of these formations is obscure but may be involved with mating.

Flight activity did not appear to be affected by moon phase, moonlight, humidity, dew, wind speed or wind direction. During light rainfall, flight activity was unaffected but, during intermediate to severe rainfall, flight activity was reduced. If moderate or severe rainfall stopped between sunset and ca. 4.5 h post-sunset, flight activity resumed. If rain stopped after ca. 4.5 h post-sunset, flight activity was negligible.

Flight activity was affected by temperature. On 19 September 1981, ambient temperature decreased from 17.7°C at 2000 to 11.9°C at 2230, when flight activity stopped. Twenty-three adults (11 males and 12 females) were picked up or touched. None of these moths were able to fly but some slowly flapped their wings once or twice. Thus, 11.9°C was designated as the lower threshold-temperature for flight activity.

In general, present observations of flight activity agree with previous observations of feral adults (see Watson 1915, 1916a, 1916b, Douglas 1930, Ellisor 1942, Greene et al. 1973, Gutierrez and Pulido 1978), but do not agree with observations of colony adults (see Leppla et al. 1979, Wales 1983). Leppla et al. (1979) found a high frequency of flight during photophase of the first six days for paired adults and Wales (1983) was unable to resolve hourly patterns of flight frequency during scotophase. Results from both studies contrast sharply with present findings. Differences among the present study and those of Leppla et al. (1979), and Wales (1983) may be an artifact of adult colonization. Colonized adults apparently behave differently than wild adults.

Mating

Of the five stages in the courtship sequence reported by Greene et al. (1973), four were observed in the field: pheromone release, male

response, mounting by the male, and separation. Sperm transfer was not observed. Greene et al. (1973) must have assumed sperm transfer took place between coupled moths because they did not present their techniques for observation of this internal process. Greene et al. (1973) noted that calling females pointed their abdominal tip either dorsally or ventrally, and Johnson et al. (1981) noted wing fanning followed immediately by dorsal elevation of the abdominal tip. In present observations, "calling" females were observed rarely with an arched abdomen (ventrally or dorsally) or a protruding pheromone-gland. In "calling," a female positioned her feet on a plant surface; wings were extended horizontally, vibrated, and flattened to the substrate. Wing vibration was very rapid, lasted ca. 3-10 secs, and was difficult to observe because of the high frequency of the vibrations and the small vertical pitch of the wings (ca. 1-2°). Typically, feral females appeared to release pheromone without abdominal arching or displaying a pheromone gland. The discrepancy among present observations and those of Johnson et al. (1981) and Greene et al. (1973) is unclear but may be due to observer interference. When releasing pheromone, moths appeared "agitated" by my light and would rapidly withdraw their pheromone gland (if everted).

During courtship, a male approached a calling female by flying in a zigzag path. This zigzag flight-path was essentially horizontal, although the male gradually descended toward the female. Male flight-speed was moderate, wing beat was flutter-like, and the male hovered briefly over the female before mounting her. The time from mounting to opposing position lasted ca. 2-10 sec. A similar time ($\bar{x}$ = 5 sec) was reported by Greene et al. (1973). Opposing position was obtained when the male swung to the left, and downward, 180°; swinging may occur to

the right but was never observed. Following the swing manuver, both adults essentially were in the same horizontal plane, heads were pointed in opposite directions, and their abdominal ends were connected caudally (see Fig. 3.1). Typically, in opposing position, the female faced skyward and the male faced earthward. Males were observed with their feet on plant substrate or dangling in air.

Couples were immobile during the opposing position. If touched, couples remained immobile, walked less than 5 cm, or fell to the ground or a plant structure. In falling, adults slowly fluttered their wings. Wing movement stopped upon landing and adults became immobile. Upon separation, males flew away within ca. 5 min but females remained at the copulation site for a longer but undetermined length of time. Greene et al. (1973) noted a similar scenario of immobility during copulation and of separation activities. Typically, coupled adults were not disturbed by other adults but on two separate occasions an adult male flew into and bumped a mating pair. After several bumps the males flew away. Perhaps these females were still emitting pheromone.

In 1981, 7 pairs of adults were timed for length of opposing position. All pairs were found on soybean within one hour after sunset, and all pairs had coupled prior to their location (except for one pair). These adults may have been coupled for an hour prior to their location, but mating was uncommon in the first .5 h after sunset and was never observed during photophase (see below). Opposing position was maintained for 2 h 10 min ± 32 min ($\bar{x}$ ± SD), and this time closely agrees with that reported by Greene et al. (1973).

Adults in opposing position were observed 157 times, with 135 on soybean, 11 on beggarweed [Desmodium tortuosum (Sw.) DC.], 9 on hairy indigo (Indigofera hirsuta L.), and 2 on bahiagrass (Paspalum notatum

Figure 3.1. Mating pair of adult velvetbean caterpillar on a soybean leaflet. Adults are in opposing position, with the male facing downward, or earthward. Photograph taken at Green Acres Research Farm, University of Florida, Alachua County, FL, 19 September 1982.

Flugge). On soybean and beggarweed, each pair was found on a leaflet. On hairy indigo, one of the opposing pairs was observed on developing seeds. The other eight pairs were found with each pair on several leaflets; a hairy indigo leaflet is smaller than a VBC adult. On bahiagrass, each opposing pair was observed on a raceme. Of the records that were kept of adult position on leaflets, the following can be noted: (1) for soybean, 29 pairs were on the bottom and 2 pairs on the top, (2) for beggarweed, 4 pairs were on the bottom and 5 pairs on the top, and (3) for hairy indigo, 1 pair was on the bottom and 1 pair on the top. No definite preference between leaflet top and bottom was noted for beggarweed or hairy indigo. A definite preference for the bottom of a soybean leaflet was noted. The relevance of this preference is unknown, but it may be a behavioral trait to avoid predation. Moths mating on the bottom of a leaflet are more difficult to see than moths on the top of a leaflet. As moths are docile and immobile during mating, adults on the top of a leaflet may be seen and preyed upon more readily by predators.

Mating occurred exclusively on legume plants, except for 2 pairs in 1980 that mated on bahiagrass at the field edge. Of the 157 observed-pairs of coupled adults, 135 pairs (ca. 86%) mated on soybean, 11 pairs (ca. 7%) mated on beggarweed, and 9 pairs (ca. 6%) mated on hairy indigo. All matings on beggarweed and hairy indigo were observed in 1982, except for one pair on beggarweed in 1981.

A shift in mating site appeared to occur in late September, 1982. Limited observations in late September of 1980 and 1981 prohibited the disclosure of such a shift during those years. In 1982, the shift appeared to be from soybean to hairy indigo. Mating occurred on soybean

in August and September and on hairy indigo in late September in a fallow border area (see Appendix C, Table C.3). The border area was composed predominately of hairy indigo plants that were tall (ca. 1.5 m) and exhibited lush, thick vegetative growth. The shift from soybean to hairy indigo may have occurred for three reasons. First, a high moisture level is required for VBC mating (Leppla 1976). The hairy indigo appeared to maintain a high moisture microclimate, while soybean was senescing. Many leaves had fallen from the soybean and moisture around the plants was decreasing (see Chapter IV). Secondly, hairy indigo was an ovipositional site (see below). Soybean received a low complement of VBC eggs in late September (see Chapter V). Thirdly, female VBC may have been attracted to the height of the hairy indigo plants. VBC tended to mate on soybean at a height of ca. .8 m or higher. "Calling" at this height may have increased mating success through better pheromone dispersal.

Mating was observed only during scotophase, between sunset and sunrise, from 1980-82 (see Appendix C, Table C3). Mating may have occurred during photophase (sunrise to sunset), but this occurrence is doubtful, except for times close to sunset. Low levels of moisture at the canopy top during photophase should inhibit mating during photophase (see Leppla 1976 and Chapter IV). Also, predation of mating moths should be higher during photophase, as moths would be visually exposed and immobile.

Based on the percent-normalized sample means of the weighted observations, 79.25% of all mating occurred within the first four hours after sunset [see Fig. 3.2(A) and Appendix C, Table C.4]. Greene et al.

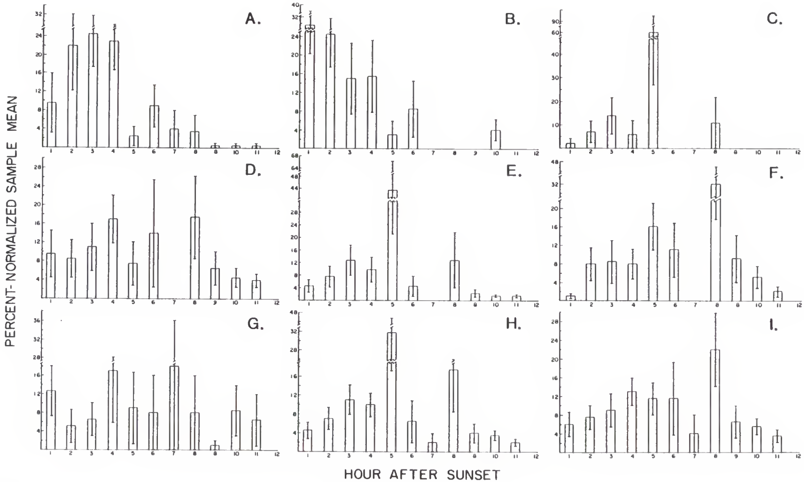

Figure 3.2. The percent-normalized sample mean (± SE) of each post-sunset hour for activities of adult velvetbean caterpillars: (A) mating, (B) oviposition, (C) feeding, males in aggregations, (D) feeding, males not in aggregations, (E) feeding, all males, (F) feeding, females, (G) feeding, unsexed adults, (H) feeding, males (all), females, and unsexed adults, and (I) feeding, males (not in aggregations), females, and unsexed adults. Observations were made from 1980-82 at the Green Acres Research Farm, Alachua County, FL, in a 1 ha soybean field.

(1973) obtained similar results and found that 66%* of all mating occurred over the same time period. Both of our results contrast sharply with those of Leppla (1976), where 81%** of all mating for colony adults occurred in hours 6-10 of scotophase.

The difference in Leppla's (1976) results from the results in this study and from Greene et al. (1973) may be related to (1) colony artifact, (2) temperature and predation, (3) moisture, or (4) reproductive isolation. Colony adults may mate at a different time from feral adults due to colonization. As noted above, colony adults do behave differently than feral adults with regard to the temporal occurrence of flight. With regard to temperature and predation, colony adults are maintained at a constant temperature and are not exposed to predation. Wild adults are exposed to variable and cyclic temperatures (See NOAA 1982) and should be vulnerable to predation when mating at certain times, as moths are highly visible and very docile. If mating is temperature-dependent, more time will be required to complete mating as temperature decreases during the night. Wild moths that mate in early scotophase will complete mating before sunrise. Wild moths that mate in late scotophase probably will not complete mating before sunrise and will be exposed visually to predators. In a colony with constant temperature and a lack of predation, females may "assess" the temperature/predator risk and mate during late scotophase. Mating by colony adults in late scotophase may favor the completion of a more beneficial activity during early scotophase (e.g., oviposition). Also,

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*Percentage value determined with calculations of data in Table 1 of Greene et al. (1973, p. 1114).

**Percentage value determined with calculations of data in Fig. 3 of Leppla (1976, p. 47).

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**Percentage value determined with calculations of data in Fig. 3 of Leppla (1976, p. 47).

The temporal occurrence of oviposition in the field may be due to the selective pressures of egg predators and parasites. Eggs are mint green when laid (see below and Chapter V) and are easy to see on soybean. As eggs age, they develop a speckling pattern (see below and Chapter V) and are extremely difficult to see on a plant (i.e., speckled eggs are cryptic). The occurrence of this speckling pattern is temperature dependent (see Chapter V). Eggs laid during early scotophase speckle at or just after sunrise (see Chapter V) and probably are difficult for predators to see. Eggs laid during late scotophase are still mint green after sunrise, are easy to see, and probably are exposed to more predation. Females that oviposit in early scotophase should demonstrate a higher reproductive fitness over females that lay eggs in late scotophase.

Oviposition was difficult to observe. Only 121 sightings were made during the 153 h 13 min of scotophase observation (see Appendix C, Table C.5). Female density may have affected the viewing of oviposition. In 1982, an estimate of female absolute density in the field was obtained at weekly intervals with an adult trap-cage (Table 3.2, see also Chapter IV). Estimates of female density were highest from August 26 to September 23. Interestingly, 61 of 73 ovipositional sightings (81%) were made at this time with an investment of only 41% of total observation time (1764 of 4348 min)(see Appendix C, Table C.5). Obviously, a productive time period to view oviposition occurred when total female density was greater than ca. 764 individuals. Concentration of more observation time during this time period may have generated more sightings.

Flight speed of ovipositing females was moderate and wing beat was flutter-like. The distance between ovipositional sites varied from ca.

Table 3.2. Estimates of the absolute density of adult females of the velvetbean caterpillar in a soybean field. Density was determined with an adult trap-cage (see Chapter IV) in 1982 at the Green Acres Research Farm, Alachua County, FL.

Date	Absolute Density of Adult Females (number/.87 ha)
July 15	0
July 22	0
July 29	0
August 5	416.8
August 12	347.3
August 19	416.8
August 26	1806.2
September 2	2570.4
September 9	2292.5
September 16	694.7
September 23	764.1
September 30	208.4
October 7	347.3
October 14	416.8

.10 to 1.25 m, based on visual estimates. When ovipositing on a leaflet, a female (1) landed on the leaflet, (2) moved her abdominal tip back and forth across the leaflet surface and sometimes walked at the same time, (3) positioned her abdominal tip against a leaflet vein, (4) arched her abdomen with the abdominal tip directed downward, (5) pressed her abdominal tip against the leaflet surface and the vein, exposing the conjunctiva anterior of the ovipositor, and (6) laid an egg. Oviposition on plant structures other than leaflets followed the same procedure, with the obvious exception that eggs were not laid on leaflet veins. Time required to lay an egg varied from ca. 2 to 30 sec, and eggs were glued to the surface and trichomes of the plant structure. Twenty-four hours later, eggs were impossible to remove without crushing. Contrary to present observations, Greene et al. (1973) indicated that eggs were nearly impossible to remove immediately after oviposition and that oviposition occurred in 2-60 sec, twice as much time as observed here.

All eggs were laid singly on leaflets, pulvini, or petioles, except for 19 September 1981 (ca. 2000) when one female laid seven eggs on a leaflet and another female attempted to lay three eggs on a leaflet. Low ambient temperature (17.7°C) affected the behavior of these two females. While ovipositing, both females continuously vibrated their wings, a previously unobserved ovipositional activity. Presumably, wing vibration allowed for ovipositonal activity at this temperature; wing vibration without flight in Lepidoptera allows for activities at suboptimal temperatures (Chapman 1971). Both females vibrated their wings for ca. 1 min before flying to another leaflet. Their flight speed was very slow and wing beat was flap-like.

At 2230 on 19 September 1981, all flight and oviposition stopped when the temperature fell to 11.9°C. Twelve females were picked-up or touched and none were able to fly. Most remained very rigid and did not move, but a few flapped their wings once or twice, or took a few steps. Evidently, 11.9°C is near the lower threshold for oviposition. Overall, these observations indicate that temperature affects egg dispersion and deposition.

Greene et al. (1973) found that ovipositional activity increased with decreasing temperature. Neither my results nor those of Moscardi et al. (1981c) agree with the findings of Greene et al. (1973). Moscardi et al. (1981c) found that mean total oviposition varied significantly with temperature (Table 3.3). In a linear regression of their data and the assumed ovipositional threshold of 11.9°C* (see Fig. 3.3), a correlation (r^2 = .75, n = 74) was found between total oviposition per female and temperature with the model:

$y = -694.97 + 58.40(x)$,

where y = total oviposition per female, and

x = temperature between 11.9 and 26.7°C.

Slope and intercept parameters were determined with observations and not mean estimates, but mean estimates are shown in Fig. 3.3 for ease of view. The regression line was forced through the x intercept at 11.9°C.

No other weather factors besides photophase and temperature were observed visually to affect oviposition (i.e., humidity, rainfall, moonlight, wind speed and wind direction). Greene et al. (1973) found

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*Data used in the regression are listed in Appendix C, Table C.7. Data of Moscardi et al. (1981c) were stored on computer cards in Building 175, Insect Population Dynamics Laboratory, at the University of Florida, Gainesville, FL, at the time that this regression model was calculated.

Table 3.3. Mean total oviposition by adult females of the velvetbean caterpillar reared from eggs at constant temperatures, 14L:10D photoperiod, and RH > 80% (modified from Moscardi et al. 1981c).

Temperature (°C)	Number of Mated Females	Mean Total-Eggs/Female (± SE)[a]
21.1	19	482.8 ± 21.3C
23.9	29	732.3 ± 22.9B
26.7	25	842.2 ± 26.1A
29.4	15	713.5 ± 28.1B
32.2	19	310.0 ± 14.7D

[a]Means followed by the same letter are not significantly different according to Duncan's multiple range test (α = .05).

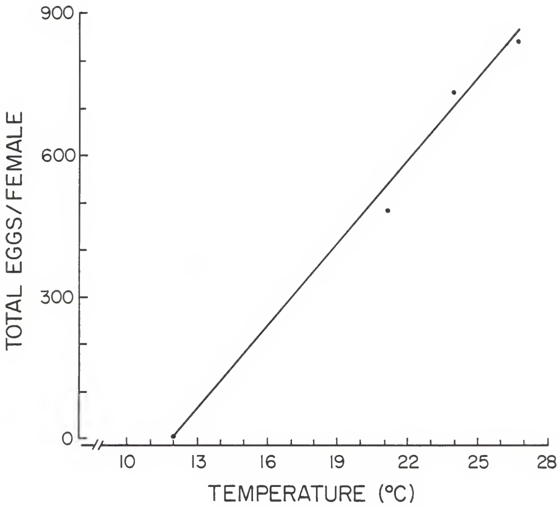

Figure 3.3. Linear relationship between total eggs per velvetbean caterpillar adult female and temperature. Regression line is $y = -694.97 + 58.40(x)$, ($r^2 = .75$, $n = 74$), where y = total oviposition per female, and x = temperature between 11.9 and 26.7°C. Mean estimates are shown in the figure for ease of view. Data are from Moscardi et al. (1981c), while the assumed threshold temperature is from field observations at Green Acres Research Farm, Alachua County, FL.

oviposition was more common as RH increased and less common as dew formed during scotophase. Current observations do not support the findings of Greene et al. (1973) for the following reasons: (1) RH during the first hour after sunset was typically lower than all other hours during scotophase (see NOAA 1982), (2) the highest percentage of oviposition [29%, see Fig. 3.2(B)] occurred during the first hour post-sunset, and (3) females were observed frequently to oviposit after dew set.

Fifty-four of the 121 ovipositional sites were searched for eggs; at 20 sites eggs were found, at 34 sites no eggs were found, and no search was made at 67 sites. Greene et al. (1973) noted also that females exhibit ovipositional behavior without leaving an egg. The nature of this behavior is obscure, but at least three possible explanations exist: (1) eggs may not adhere to substrate, (2) females may lack a proper ovipositional cue, and (3) females might leave egg kairomones that may "confuse" egg predators and parasites.

Of the twenty sightings at which an egg was laid, all eggs were light green in color. Twenty-four hours later, all eggs had numerous small reddish-brown speckles over a light-green background color. These small reddish-brown speckles indicated egg viability (see Chapter V).

Oviposition was observed on soybean 48 times (1981) and 72 times (1982), and on hairy indigo one time (1982). On soybean, all ovipositions occurred on leaflets except for one sighting each on a pulvinus and on a petiole. Fourteen records were kept of egg placement on leaflets. Thirteen eggs were placed by main veins and one egg was placed by a secondary vein. All eggs were glued to the plant substrate and to closely associated trichomes. Trichome density on the leaflets

was highest along the main vein and less dense along the secondary veins. Pulvini were covered in a thick "carpet" of trichomes and petioles had trichomes that occurred in longitudinal rows. Both Hinds (1930) and Ellisor (1942) noted an ovipositional preference for areas of high trichome density.

Feeding

More individuals were observed feeding than for any other activity. A total of 458 individuals were sighted: 268 males, 129 females, and 61 unsexed adults (Table 3.4). Unsexed adults flew away before a positive sexual identification could be made. Feeding occurred predominately at night, when 448 of the moths (or 98%) were observed (Table 3.4).

When feeding, the proboscis was extended, touched the food source, and was maneuvered across the food source surface. Except for flowers, all moths were observed to feed on moist surfaces. This moisture was either rain water, dew, plant-guttated water, or plant exudates. When feeding at a flower, a moth would probe the flower with its proboscis. The attainment of nectar or pollen was not assessed. No adults were observed to feed at soybean flowers and none of the food sources were chemically analyzed.

Overall, feeding was the easiest behavioral activity to observe. At night, adults were easy to approach and observe. Individuals "rested" on an available substrate while feeding, as opposed to flying. During the day, adults were more difficult to approach and observe. On six occasions, moths were observed feeding at flowers (Table 3.5). These moths hovered in flight while feeding, were in the open, and were easy to see. When approached from ca. 1.5 m moths stopped feeding, flew a short distance and "hid" among weeds. Apparently, adults can see very

Table 3.4. Number of unsexed, male, and female adults of the velvetbean caterpillar observed feeding in a soybean field at Green Acres Research Farm, Alachua County, FL, in 1980-82.

Temporal Occurrence	Unsexed[c] Adults	Male	Female	Total
Photophase[a]	8	1	1	10
Scotophase[b]	53	267	128	448
Total	61	268	129	458

[a]Photophase = sunrise to sunset.

[b]Scotophase = sunset to sunrise.

[c]Unsexed adults flew out of sight before sexual identification could be made.

Table 3.5. Observational records of feeding by adult velvetbean caterpillar during photophase at the Green Acres Research Farm, Alachua County, FL, from 1980-83.

Date	Time of Sunset	Time of Observation	Time Before Sunset (h/min)	Number of Adults	Adult Sex[a]	Food Source[b]
19 September 1980	1930	1900	0/30	2	Adult	Horse Mint
20 September 1980	1928	1900	0/28	2	Adult	Horse Mint
24 September 1982	1923	1900	0/23	2	Adult	Hairy Indigo
02 October 1982	1914	1515	3/59	1	Female	Hairy Indigo
				2	Adult	Hairy Indigo
02 October 1982	1914	1535	3/39	1	Male	Hairy Indigo
08 November 1983[c]	1739	1730	0/09	2	Female	Common Beggar Tick

[a]Sexually unidentified moths are listed as adult.

[b]The food source was always at a flower.
Horse Mint is <u>Monarda punctata</u> L.
Hairy Indigo is <u>Indigofera hirsuta</u> L.
Common Beggar Tick is <u>Bidens alba</u> (L.) DC.

[c]Observed on the campus of the University of Florida, Gainesville, FL.

well in daylight or detect human presence. Why these moths stopped feeding and flew is unknown.

A definite preference for feeding sites at the edge of the field (± ca. 2 m) was exhibited, where ca. 57% (261 of 458 adults) of all feeding was observed. Of the 197 observations in the field, 163 were of adult males at human-altered feeding sites. Re-examination of the data without these human-altered sites reveals that ca. 88% (261 of 295 adults) of all feeding occurred at the edge of the field. Due to the strong bias of feeding at field-edge sites, and because most observation time was spent in the field and not at the field edge, results on the temporal occurrence of feeding should be viewed with caution. Proper assessment of the temporal occurrence of feeding should be examined with a separate study.

Adults fed at numerous sites (Tables 3.6-3.8). The most striking feature about site selection was the dichotomy between male and female sites. Although males and females shared common sites (Table 3.7), some sites were visited strictly by males (Table 3.8). At these sites, males were observed usually in aggregations of two or more individuals (see Figs. 3.4 and 3.5). Of the 179 males at these sites, 159 were found in aggregates, and 121 of these aggregated males were on aerial and sweep nets (bags and poles). These nets were used frequently in the field (soybean and fallow areas) to collect arthropods, were stained heavily with arthropod and plant substances, and were coated with human sweat and oil. The Saran Screens, additional sites of male aggregations, were handled also by people and coated with human sweat and oil. Male aggregations were observed only at human-altered sites and not at naturally occurring sites. When feeding in aggregates, males were

Table 3.6. Number of unsexed adults[a] of the velvetbean caterpillar observed feeding in a soybean field at Green Acres Research Farm, Alachua County, FL, in 1980-82. Description of food site and host provided.

No. of Unsexed Adults Feeding[b]	Food Site[c]	Food Host		
		Common Name	Scientific Name	Family
4	Flower	Horse Mint	*Monarda puntata* L.	Labiatae
43	Raceme	Bahiagrass	*Paspalum notatum* Flugge	Gramineae
2	Raceme	Unknown Grass	---	Gramineae
1	Flower, Unopened	Florida Pusley	*Richardia scabra* L.	Rubiaceae
6	Flower, Outside	Hairy Indigo	*Indigofera hirsuta* L.	Leguminosae
5	Flower	Hairy Indigo	*Indigofera hirsuta* L.	Leguminosae

[a] Unsexed adults flew out of sight before a positive sexual identification could be made.

[b] Total = 61.

[c] Adults fed at the surfaces of plant structures or in flowers.

Table 3.7. Number of male and female adults of the velvetbean caterpillar feeding in a soybean field at Green Acres Research Farm, Alachua County, FL, from 1980-82. Description of food site and host provided.

No. of[a] Males Feeding	No. of[b] Females Feeding	Food Site[c]	Food Host		
			Common Name	Scientific Name	Family
1	1	Seed	Slender Amaranth	*Amaranthus viridis* L.	Amaranthaceae
50	84	Raceme	Bahiagrass	*Paspalum notatum* Flugge	Gramineae
12	11	Leaflet	Soybean	*Glycine max* (L.) Merr.	Leguminosae
3	2	Leaflet, Dead	Soybean	*Glycine max* (L.) Merr.	Leguminosae
0	1	Stem, Dead	Unknown Plant[d]	---	---
3	2	Leaflet, Dead	Beggarweed	*Desmodium tortuosum* (Sw.) DC.	Leguminosae
2	2	Roots, Stems, Dead	Beggarweed	*Desmodium tortuosum* (Sw.) DC.	Leguminosae
1	0	Seed	Beggarweed	*Desmodium tortuosum* (Sw.) DC.	Leguminosae
0	1	Seed	Florida Pusley	*Richardia scabra* L.	Rubiaceae
3	2	Leaflet	Sicklepod	*Cassia obtusifolia* L.	Leguminosae
2	2	Flower, Outside	Hairy Indigo	*Indigofera hirsuta* L.	Leguminosae
1	1	Flower, Outside, Dead	Hairy Indigo	*Indigofera hirsuta* L.	Leguminosae
9	18	Flower	Hairy Indigo	*Indigofera hirsuta* L.	Leguminosae
2	0	Leaflet	Hairy Indigo	*Indigofera hirsuta* L.	Leguminosae
0	2	Leaflet, Dead	Hairy Indigo	*Indigofera hirsuta* L.	Leguminosae
0	2	Flower	Common Beggar Tick	*Bidens alba* (L.) DC.	Compositae

[a]Total males = 89.

[b]Total females = 131.

[c]Adults fed at the surfaces of plant structures or in flowers.

[d]Dicotyledonous plant.

Table 3.8. Number of adult males of the velvetbean caterpillar feeding in a soybean field at Green Acres Research Farm, Alachua County, FL, from 1980-82. Also, number of males per aggregate, number of aggregates, and description of food site are provided.

No. of[a] Males Feeding	No. of Males[b] Per Aggregate	No. of[c] Aggregates	Description of Food Site[d]
5	0	0	Human Skin
4	0	0	Vinyl Raincoat
1	0	0	White Cotton Pants
1	0	0	Aluminium Push Button, Head Lamp
3	0	0	Bamboo Sticks
123	29, 22, 18, 17, 12, 9, 5, 3, 3, 3	10	Aerial and Sweep Nets (Bag and Pole)
16	15	1	Black Saran Screen
24	15, 5, 3	3	Brown Saran Screen
2	0	0	Barb Wire Fence

[a]Total Male Feeding = 179.

[b]Total Males in Aggregates = 159.

[c]Total Aggregates = 14.

[d]Males fed at the surfaces of food sites.

Figure 3.4. Aggregation of velvetbean caterpillar males on an aerial net. Males are feeding at the surface of the net (bag and pole). Photograph was made in a 1 ha soybean field at the Green Acres Research Farm, Alachua County, FL, September 7, 1983.

Figure 3.5. Aggregation of velvetbean caterpillar males on the screen of an insectary. Males are feeding at the surface of the screen. Photograph was taken at the edge of a 1 ha soybean field at the Green Acres Research Farm, Alachua County, FL, September 14, 1983.

extremely docile and could be touched frequently without cessation of feeding. How males were attracted to these sites is unknown, but they may have utilized these sites to acquire salts, as some male lepidoptera aggregate and acquire salts (see Arms et al. 1974).

The most prevalent feeding site was the raceme of bahiagrass, accounting for 177 (39%) of all observations (see Tables 3.4, 3.6 and 3.7). Fifty males and 84 females were observed, for a sex-bias ratio of 1:1.7 (male to female). The nature of this bias (if valid) is unknown, as is the nutritional source obtained on or from the bahiagrass. An adult is shown feeding at a raceme of bahiagrass in Fig. 3.6. Adults fed frequently on legumes, accounting for 99 (22%) of the observations (see Tables 3.4 and 3.5-3.7). No sexual bias was noted. These adults may have acquired various plant compounds, but the compounds and their utilization are unknown. Nineteen adults fed at dead plant tissue, and no sexual bias was exhibited (see Table 3.7 and Fig. 3.7). With one exception, these dead tissues were all from legumes. The compounds acquired from these dead plant tissues, as well as their utilization, are unknown. Some moths of the Ctenuchidae and Arctiidae feed on dead and withered plants as a possible nitrogen source (see Goss 1979).

The occurrence of males feeding in aggregations was an uncommon sight in the field and contributed to the large standard errors shown in Fig. 3.2(C) (see also Appendix C, Table C.9). Male aggregations may have been found more often if an effort had been devoted solely to aggregate location during each observation period. Observation of additional aggregates may have resulted in smaller standard errors, as well as a different temporal pattern in their occurrence. Nevertheless, males were prevalent in aggregates during the fifth hour after sunset

Figure 3.6. Adult velvetbean caterpillar feeding at the surface of a bahiagrass raceme. Photograph was made at the edge of a 1 ha soybean field on the Green Acres Research Farm, Alachua County, FL, 16 September 1985.

Figure 3.7. Adult velvetbean caterpillar feeding at the surface of a dead soybean leaflet. Photograph was made in a soybean field in Melrose, FL, Alachua County, 7 October 1983.

when ca. 60% of all aggregated males were observed. Interestingly, almost all mating (79.25%) occurred in the first four hours after sunset, but the adaptive significance of the temporal relationship between mating and aggregating is obscure.

Feeding by non-aggregated males occurred throughout scotophase, except for the seventh hour when no feeding was recorded [Fig. 3.2(D) and Appendix C, Table C.10]. Feeding by males probably occurred in the seventh hour but only four observational periods were completed at this time. The temporal occurrence of feeding by all males (aggregated and non-aggregated) was non-uniformly distributed throughout scotophase, as ca. 82% occurred within the first 6 h after sunset [see Fig. 3.2(D) and Appendix C, Table C.11]. This non-uniform distribution was dominated by the fifth post-sunset hour (43.65%) when large numbers of males aggregated. Leppla (1976) found that colony males fed uniformly throughout scotophase.

The temporal occurrence of feeding by females was non-uniformly distributed, as 74.67% occurred between hours 5 and 11 post-sunset [see Fig. 3.2(F), Appendix C, Table C.12]. The sample mean of hour 8 accounted for 32% of all female feeding, but why is unknown. Interestingly, the first four hours post-sunset appeared to be devoted to mating and oviposition when 79.25% and 84.72% of each activity occurred, respectively. Females apparently partitioned their time between feeding, mating, and ovipositing and may have acquired an increased reproductive fitness from this partitioning (i.e., ovipositing and mating during early scotophase may be more beneficial than feeding). Leppla (1976) found that colony females fed throughout scotophase but that feeding increased during the second half of scotophase.

The temporal occurrence of feeding by unsexed adults was reasonably uniform throughout the night [see Fig. 3.2(G) and Appendix C, Table C.13]; unsexed adults flew out of sight before a positive sexual identification could be made. The uniform inability to sexually identify adults indicates no temporal bias occurred in identification of unsexed adults during scotophase. The occurrence of feeding by all adults (males, females, and unsexed) differed noteable for hours five, eight, and twelve [see Fig. 3.2(H) and Appendix C, Table C.14]. These hours corresponded, respectively, to peaks in male (aggregated) and female feeding and to no feeding at all. The feeding occurrence of males (not aggregated), females, and unsexed adults was different, particularly for the eighth hour, which corresponded to peak female feeding [see Fig. 3.2(I) and Appendix C, Table C.15]. Overall, feeding by VBC adults occurred at all hours of the night (except for the 12th hour).

Predators

Spiders were the only observed predators of VBC adults. No effort was made to identify all the spider species at the study site or to obtain density estimates of the recorded spider predators. Peucetia viridans (Hentz) and Misumenops spp. were the most frequently observed spiders. Peucetia viridans was found throughout the field (edge and interior), usually on dicotyledonous plants and high above the ground (ca. 1 m or higher). Misumenops spp. were found only at the field edge, usually on monocotyledonous plants and close to the ground (ca. .5 m or less). Most of the orbweavers were found at the field edge, with webs at a height between ca. .5 and 1.5 m.

Six species of spiders were recorded as predators, with 26 predation records (see Table 3.9); all records were obtained during

Table 3.9. Records of spider predation on adult velvetbean caterpillar (VBC) from 1980-83 at Green Acres Research Farm, Alachua County, FL, in a 1 ha soybean field. All records occurred during scotophase.

Date[a] (D-M-Y)	Time[b]	Location[c]	Spider Scientific Name[d]	Spider Common Name	Spider Family	Spider[e] Stage and Sex	VBC[f] Adult Sex
19-S-81	2047	E, Bahiagrass	Peucetia viridans (Hentz)	Green Lynx	Oxyopidae	*, +	M
19-S-81	2058	I, Soybean	Peucetia viridans (Hentz)	Green Lynx	Oxyopidae	*, +	M
24-S-82	2112	I, Florida Pasley	Peucetia viridans (Hentz)	Green Lynx	Oxyopidae	*, +	M
17-S-81	2115	E, Bahiagrass	Peucetia viridans (Hentz)	Green Lynx	Oxyopidae	*, +	F
19-S-83	2130	E, Sandbur	Peucetia viridans (Hentz)	Green Lynx	Oxyopidae	*, *	M
24-S-82	2147	I, Soybean	Peucetia viridans (Hentz)	Green Lynx	Oxyopidae	*, +	F
24-S-82	2223	I, Soybean	Peucetia viridans (Hentz)	Green Lynx	Oxyopidae	*, +	F
09-S-81	2303	I, Soybean	Peucetia viridans (Hentz)	Green Lynx	Oxyopidae	*, +	M
03-S-82	2323	E, Beggarweed	Peucetia viridans (Hentz)	Green Lynx	Oxyopidae	A, +	M
03-S-82	2340	I, Sicklepod	Peucetia viridans (Hentz)	Green Lynx	Oxyopidae	A, +	M
25-S-82	0023	I, Hairy Indigo	Peucetia viridans (Hentz)	Green Lynx	Oxyopidae	*, +	M
04-S-82	0052	I, Soybean	Peucetia viridans (Hentz)	Green Lynx	Oxyopidae	A, +	M
04-S-82	0111	I, Sicklepod	Peucetia viridans (Hentz)	Green Lynx	Oxyopidae	A, F	M
04-S-82	0136	I, Soybean	Peucetia viridans (Hentz)	Green Lynx	Oxyopidae	*, +	M
21-A-81	0545-0701	I, Soybean	Peucetia viridans (Hentz)	Green Lynx	Oxyopidae	I, +	+
25-A-81	0545-0703	E, Grass	Peucetia viridans (Hentz)	Green Lynx	Oxyopidae	*, +	M
15-S-81	0545-0714	I, Soybean	Peucetia viridans (Hentz)	Green Lynx	Oxyopidae	*, +	M
03-S-81	2230	E, Bahiagrass	Misumenops celer (Hentz)	Crab	Thomisidae	A, +	M

Table 3.9 (continued)

Date[a] (D-M-Y)	Time[b]	Location[c]	Spider Scientific Name[d]	Spider Common Name	Spider Family	Spider[e] Stage and Sex	VBC[f] Adult Sex
16-A-81	0000-0700	E, Grass	Misumenops celer (Hentz)	Crab	Thomisidae	A, +	M
09-0-82	0530	E, Hairy Indigo	Misumenops celer (Hentz)	Crab	Thomisidae	A, +	M
01-S-81	0545-0607	E, Grass	Misumenops celer (Hentz)	Crab	Thomisidae	A, +	F
15-S-81	0545-0714	E, Bahiagrass	Misumenops formocipes (Walckenaer)	Crab	Thomisidae	A, F	M
17-S-81	2100	I, Soybean	Eriophora ravilla (C. L. Koch)	Orbweaver	Araneidae	A, F	M
24-S-82	2332	E, Soybean	Neoscona arabesca (Walckenaer)	Orbweaver	Araneidae	A, F	M
05-0-82	0550	E, Soybean	Neoscona arabesca (Walckenaer)	Orbweaver	Araneidae	A, +	M
15-S-83	0200	E, Bahiagrass	Acanthepeira sp.	Orbweaver	Araneidae	I, +	F

[a]D-M-Y = Date, Month, Year; A = August, S = September, O = October; 81 = 1981, 82 = 1982, 83 = 1983.

[b]If the exact time of a predation record is not given, the record occurred during the hyperated times.

[c]E = Edge of field; record was observed within ± 1 m of the field edge. I = Inside field; record was observed in the field and at least 1 m from the field edge. Grass = unidentified grass. Bahiagrass = Paspalum notatum Flugge. Hairy Indigo = Indigofera hirsuta L. Soybean = Glycine max (L.) Merr. Beggarweed = Desmodium tortuosum (Sw.) DC. Sicklepod = Cassia obtusifolia L. Florida Pusley = Richardia scabra L. Sandbur = Cenchrus sp.

[d]Except for P. viridans, all spiders were identified by Dr. G. B. Edwards, Taxonomic Acarologist and Curator, Florida State Collection of Arthropods, Gainesville, FL. P. viridans' were identified by the author, but four of these specimens were reconfirmed by Dr. Edwards.

[e]I = immature, A = adult, F = female, * = undetermined stage, + = undetermined sex.

[f]+ = undetermined sex, M = male, F = female

scotophase. A male-prey bias exists, as 20 of 26 prey were males; adult VBC sex-ratio was ca. 1:1 (see Chapter IV). The nature of this bias is unknown but may be due to aggressive chemical mimicry of VBC mating-pheromone by some or all of these spiders (see Foelix 1982).

Most of the predation records, 17 out of 26 (65%), were of *P. viridens*. Fourteen of these records occurred between 2047 and 0136, the time period when VBC adults were most active. *Misumenops* spp. accounted for 5 of the 26 records (19%) and the orbweavers accounted for 4 of the 26 records (15%). The large number of *P. viridens* records may be a reflection of where observation time was concentrated (i.e., in the field). Also, the webs of orbweavers were destroyed frequently by research personnel walking through the field. Figures 3.8 and 3.9 are photographs of two spider predation records.

Conclusions

The temporal patterns of several adult activities (flight, mating, oviposition, and feeding) were observed and quantified in the present study, as were some environmental factors that affected these patterns. The suspected adaptive significance of these activity patterns was discussed. Flight occurred primarily at night. During the day, adults resided in the field but only after the soybean canopy had begun to close or was closed. During the day adults flew only when disturbed or rarely if feeding. Approximately 79% of all mating occurred within the first four hours of scotophase. Mating occurred usually at the top of soybean plants, a height of ca. .8 m. Placement of pheromone traps near the canopy top in the field would result probably in the largest capture of males. Approximately 96% of all oviposition occurred within the first six hours of scotophase and feeding occurred primarily at night. Females utilized nutritional sources that may have affected egg

Figure 3.8. Green lynx spider [Peucetia viridans (Hentz)] preying on an adult male velvetbean caterpillar. Photograph was made at the edge of a 1 ha soybean field at the Green Acres Research Farm, Alachua County, FL, 19 September 1983.

Figure 3.9. Orbweaver spider (Acanthepeira sp.) preying on an adult female velvetbean caterpillar. Photograph was made at the edge of a 1 ha soybean field at the Green Acres Research Farm, Alachua County, FL, 15 September 1983.

production. Males utilized some food sources that females did not use. At these sources, males usually occurred in aggregations. Future research efforts might examine more quantitatively the affect of adult age, adult nutrition, host plant density and physiology, and weather factors on flight, mating, oviposition, and feeding. Some of these efforts might be accomplished by observing individual moths.

Observations of adult activities were density-dependent. Sightings of mating, oviposition, feeding, and mortality were not observed in June and July at low adult density, but were observed in August, September, and early October at high adult density (see Chapter IV for adult density data). In future studies of adult behavior, concentration of observation time during high adult density should yield more behavioral observations.

The present study has expanded our knowledge of VBC behavior and provided information essential for the construction of a model of adult and egg populations (see Chapter VI). Knowledge of the temporal occurrence of flight and some environmental factors affecting flight allowed for the development of an unique adult sampling method (and the subsequent acquisition of adult density data) and a better understanding of adult density fluctuations (see Chapter IV). Knowledge of the temporal occurrence of oviposition allowed for the development of an unique sampling method for eggs and the subsequent acquisition of egg density data (see Chapter V). The measurements of adult and egg densities are presented in the next two chapters. These density measurements were necessary for model construction and validation (see Chapter VI).

CHAPTER IV
MEASUREMENT AND ANALYSIS OF INTRAFIELD ACTIVITY OF ADULT VELVETBEAN CATERPILLAR

Introduction

The velvetbean caterpillar (VBC) is believed to "overwinter" in much of the Caribbean Basin and South America and is conjectured to move annually into the southern United States (Watson 1916a, Herzog and Todd 1980, Buschman et al. 1981a). The magnitude and timing of VBC immigration are unknown, as no direct evidence exists (Buschman et al. 1981a). Based on density data of larvae, adult VBC evidently invade soybean in northern Florida during late June, July and August (see Greene 1976, Menke and Greene 1976, Linker 1980). Following adult colonization, larvae reach peak densities in August - September and, occasionally, early October (Greene 1976, Menke and Greene 1976, Linker 1980). With the October onset of soybean senescence, VBC adults are suspected to move onto alternate hosts where their larvae have been collected (Ellisor 1942, Greene 1976, Buschman et al. 1981a). Larvae and pupae appear incapable of overwintering in northern Florida (Buschman et al. 1977); thus, infestation of soybean the following year depends on VBC adult immigration (see Watson 1916a, Buschman et al. 1977, 1981a).

Current management of VBC is directed at control of in-field larval densities (Linker 1980). This type of management treats the symptoms of the pest problem and not the cause (see Stimac and Barfield 1979, Barfield and O'Neil 1984). In a simulation model of soybean/VBC

dynamics, Wilkerson et al. (1983) found that changes in the density and influx timing of adults into soybean resulted in notable differences in soybean yield and grower profit (from -$289.63 to $169.21/ha)(see Table 1.1). Clearly, knowledge of when and why adults immigrate into soybean could provide a better understanding of VBC dynamics and lead to more enlightened management.

The present study was initiated to quantify and model adult and egg populations of VBC within soybean. Model construction depended on estimates of adult and egg densities. Data on adult density were essential for model initialization and data on egg density (see Chapter V) were required to assess the impact of adult reproduction in the field (i.e., the mere presence of adults does not connote the presence of eggs and resultant larval defoliators). In the present study, adult VBC density was monitored in soybean, the reproductive status of adult females was determined, and select environmental variables were monitored.

Materials and Methods

Adult Sampling

Adult VBC density was monitored (1980-82) in a 1 ha soybean field (cv. Bragg), at the University of Florida's Green Acres Research Farm (ca. 22.5 km west of Gainesville, FL, Alachua County). Specific agronomic practices and soybean phenological stages are listed in Appendix A. Adult VBC density was measured with two devices. The first device, a blacklight trap (BLT), was used in all three years, was placed in the field, and was situated 21.2 m diagonally from a field corner and 15 m from the closest field edges. The blacklight trap in 1980 did not conform to the BLT standards recommended by the Entomological Society of America, but the trap in 1981 and 1982 did meet the society's

recommendations (see Harding et al. 1966). New 15 w bulbs (General Electric F15T8-BL) were installed each field season, and the funnel top of each trap was positioned 1.5 m above the ground. Isopropanol (99%) was used as the killing agent and was changed daily (1.89 L/day). Adult VBC were segregated daily from total trap catch, counted, sexed and stored in 5% formalin.

The second adult monitoring device, an adult trap-cage, was used during the day in 1982 (Fig. 4.1). Development of this trap resulted from the observation that adults reside in the soybean field during the day (see Chapter III). Outside dimensions of the cage were 4.6 x 4.6 x 2.1 m, and the frame was constructed of 1.25 inch polyvinylchloride pipe (PVC, PR160). The frame was covered with Lumite Saran Screen (Chicopee, Style #51821000) that extended 0.3 m below the cage on all sides (i.e., extension flaps). Four people carried the cage (one at each corner) via 0.9 m handle and walked one row distant from the sampled rows. The cage covered six rows of soybean and was carried above the crop canopy to avoid the flushing of VBC adults. At each sample site, bearers dropped the cage rapidly and quickly buried the extension flaps with soil. The cage was entered via a full length zipper on one side.

Each week, six simple random samples were taken with the adult trap-cage. One hour was spent inside the cage at each sample site. To assist in the exposure and capture of adults inside the cage, all weeds were removed and soybean foliage was shaken vigorously. Adults were caught with an aerial net and placed initially in a vial of 99% isopropanol. Most adults were caught within 20 min and none were caught after 40 min. Adults were counted, sexed, and stored in 5% formalin.

Figure 4.1. Trap-cage used to collect adult velvetbean caterpillar in a 1 ha soybean field during 1982 at the University of Florida's Green Acres Research Farm, Alachua County, FL.

Female Dissections

Females from the 1981 blacklight trap were dissected and placed into four reproductive categories (i.e., physiologically aged) based on a visual assessment of fat body content, ovary development, and the number of spermatophores (see Callahan 1958). Categories were (1) unmated, no spermatophore, (2) mated, fat body content full to 1/3 depleted, (3) mated, fat body content between 1/3 and 2/3 depleted, and (4) mated, fat body content 2/3 or more depleted. These categories were established with the assumption that category 1 females had the lowest reproductive output, category 2 females had the highest, and categories 3 and 4 had successively lower outputs. Unmated females were placed into three categories: (1) full, fat body content full to 1/3 depleted, (2) medium, fat body content between 1/3 and 2/3 depleted, and (3) empty, fat body content 2/3 or more, depleted.

Physical Variables

Various physical variables were monitored during the study. Variable descriptions, monitoring devices or sources of information, monitor locations, frequency of variable readings, and years monitored are provided in Table 4.1. Mean nightly measurements of the following physical variables were regressed against BLT catch (unweighted and weighted): vapor pressure deficit,* flight temperature, moonlight illuminence, rainfall, wind speed, wind direction, and barometric pressure. Equations used to determine mean physical variable values, and those values, are given in Appendix D, Tables D.4-D.6. Weighted

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*Vapor pressure deficit is a better representation of atmospheric moisture than relative humidity (RH) because interpretation of RH values are dependent upon temperature values (Anderson 1936).

Table 4.1. Description of physical variables monitored in Alachua County, FL, in 1981-82.

Physical Variable	Monitoring Device or Source	Site[a] Location	Frequency of Reading	Year[b] Monitored
Temperature (°C)	Hygrothermograph, Weather Measure Corp., Model H311	Edge (Ambient) and Field	Continuous	81,82
Temperature (°C)	Esterline Angus[R] PD2064 Microprocessor	Edge (Ambient)	Continuous	81,82
Relative Humidity (%)	Hygrothermograph, Weather Measure Corp., Model H311	Edge (Ambient) and Field	1 h	81,82
Rainfall (cm)	Universal Recording Rain Gauge, Belfort Instr. Co., 12" chart with dual springs	Edge	Continuous	81,82
Wind Speed (m/sec)[c]	Gill, 3-cup Anemometer, R. M. Young Co., Model 12102	Edge, 6.4 m Height	15 min	81
Wind Direction[c]	Gill Microvane, R. M. Young Co., Model 12302	Edge, 6.4 m Height	15 min	81
Barometric Pressure (MB)	Mirobarograph, Weather Measure Corp., Model B211	Edge (Ambient)	Continuous	81,82
Sunset and Sunrise Times, Length of Day and Night	Oliver[d]	Alachua County, FL	24 h	80,81,82

Table 4.1 (continued)

Physical Variable	Monitoring Device or Source	Site[a] Location	Frequency of Reading	Year[b] Monitored
Moon Phase and Temporal Occurrence	Smith and Smith (1981), Vohden and Smith (1982)	Alachua County, FL	Nightly	81,82
Proportional Moonlight Intensity (lumens/m^2)	Gardiner (1968)	Alachua County, FL	Nightly	81,82
Opaque Cloud Coverage	NOAA (1981; 1982)	Alachua County, FL	Nightly	81,82

[a] Edge was within 50 m of the field edge. Ambient was at a height of 1.5 m. Field was within the field, at least 15 m from nearest field edge, and at a height of .2 m.

[b] 81 = 1981; 82 = 1982.

[c] Actual readings were recorded by the Esterline Angus PD2064 Microprocessor.

[d] J. P. Oliver, Associate Professor of Astronomy, Department of Astronomy, University of Florida, Gainesville, FL 32611.

values of BLT catch were determined with the equation:

$$WBLT = (RBLT - SBLT)/(SBLT),$$

where WBLT = weighted blacklight trap catch,

RBLT = raw blacklight trap catch, and

SBLT = smoothed blacklight trap catch.

Weighted values of BLT catch represent the change in the proportional magnitude of moths captured per night in the BLT. Smoothed values were determined with a nonlinear data smoothing algorithm (3RSSH, twice) based on running medians (see Velleham 1980, Ryan et al. 1982). Three variable selection procedures were utilized: forward selection, backward elimination, and maximum r^2 improvement (i.e., forward selection with pair switching). Models were selected based upon parameter significance, residual plots, r^2, and Mallows' Cp statistic [for discussions of Cp see Mallows (1973) and Daniel and Wood (1980)].

Results and Discussions

Blacklight Trap

The total number of females, males, and adults (females and males) captured per night (1980-82) in the BLT are shown in Fig. 4.2 (A-C) and listed in Appendix D, Tables D.1-D.3. Comparisons of the number of captured moths among years are difficult to make because of (1) differences in BLT sizes, (2) electrical problems with the '80 BLT that resulted in no catch during 9 nights, and (3) variation in the temporal occurrences of trapping--the BLT ran for 71 days in '80, 116 days in '81, and 123 days in '82. Nevertheless, initially-captured adults were females in '80, males in '81, and both sexes in '82. Apparently, both sexes make initial flights into soybean. Adult density during July and August (Julian date 182 to 243) varied considerably among years. In 1981, BLT catch was depressed as only 698 adults were captured. In '80

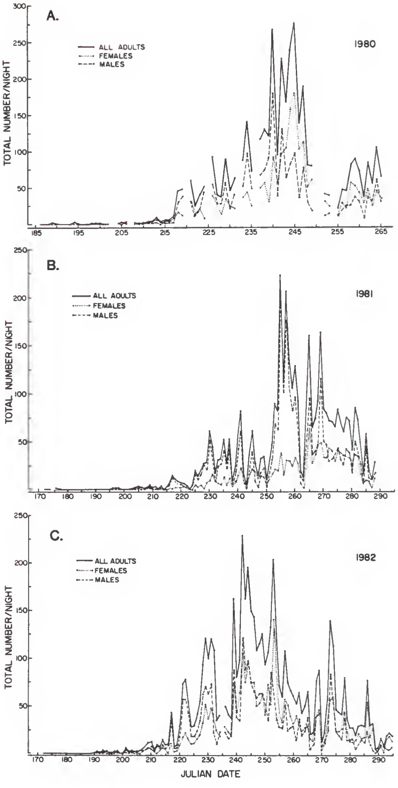

Figure 4.2. Total number of velvetbean caterpillar moths captured in a blacklight trap per night in a 1 ha soybean field at the Green Acres Research Farm, Alachua County, FL: (A) 1980, (B) 1981, and (C) 1982.

and '82, ca. three times that number were captured (2106 and 1989 adults, respectively). At this time of the field season, most of these adults were moving into the field from outside sources. Differences in the number of captured adults among years may have been due to the amount of rainfall in the general area; adult dynamics are sensitive to moisture (see Leppla 1976). In July and August of '81, 20 cm of rain fell, while in '80 and '82 ca. 30 cm of rain fell or ca. 33% more rain (see Table 4.2). Rainfall for all three years was below normal, but July and August in '81 were particularly dry with less than half of the 70 year mean.

In '80, males were the predominant BLT catch during the first half of the field season and females were predominant in the latter half. In '81 males were the predominant catch throughout the field season and in '82 both sexes were equally predominant [see Fig. 4.2 (A-C)]. The reason for variation in sex predominance between years is unknown.

Adult appearance in the field was synchronized with the appearance of eggs. In '81, eggs were found on July 24 (date 205) and consistently thereafter (see Chapter V). Adults were captured consistently from July 22 (date 203). The first adult female was captured on this same date [see Fig. 4.2(B) and Appendix D, Table D.2]. In '82, eggs were found initially on July 6 (date 187) and consistently after July 17 (date 198)(See Chapter V). Adults were captured consistently from July 9 (date 190)[see Fig. 4.2(C) and Appendix D, Table D.3].

Female Dissections

All females captured in the BLT in 1981 were dissected and placed into four reproductive categories (see Materials and Methods). A total of 1288 females were dissected. Category 2 contained the largest number of females (543), category 3 had the next largest (376), and categories

Table 4.2. Amount of rainfall recorded at the number 3 WSW climatological station of the University of Florida, Gainesville, FL, Alachua County. Cooperative climatological station of the Agronomy Department and NOAA.

Month	Rainfall (cm) 1980	1981	1982	Normal[a] Rainfall (cm)
July	22.00	7.39	17.17	20.40
August	8.08	12.65	15.70	20.96
Total	30.08	20.04	32.87	41.36

[a]Normal is 70 year mean.

4 and 1 contained smaller numbers (207 and 162, respectively); all mated females (1126) contained mature and/or maturing eggs. Seventy-one percent of all females belonged to categories 2 and 3. The total number of females per category per night mirror similar results (see Fig. 4.3). Based on BLT catch and dissections, most of the females in the field on any given night were females with high reproductive potential.

Only mated females (categories 2 and 3) were caught initially. Apparently, they moved into the field seeking oviposition sites*. Unmated females were caught in increasing numbers after date 241, and may have been individuals that completed their immature development in the field. Adult generations in another noctuid pest of soybean, the green cloverworm [Plathypena scabra (Fabricius)], have been indicated by cyclic patterns of unmated females (see Buntin and Pedigo 1983), but these cyclic patterns were not apparent in 1981 with VBC females (see Fig. 4.3).

Unmated females were placed into three categories (see Materials and Methods). Full and medium categories had essentially the same total number of individuals (78 and 79, respectively), while the empty category had only five individuals. The total number of unmated females per category per night mirror similar results (see Fig. 4.4). Based on BLT catch and these dissections, most unmated females in the field should demonstrate a high reproductive output after mating. Also, most females mated before their fat body had been depleted.

Spermatophores were removed from all mated females (1126) caught in the BLT during 1981 with the following results: 1587 spermatophores were counted, females contained one to four spermatophores, and the mean

*Eggs were first found in the field on date 205 (see Chapter V).

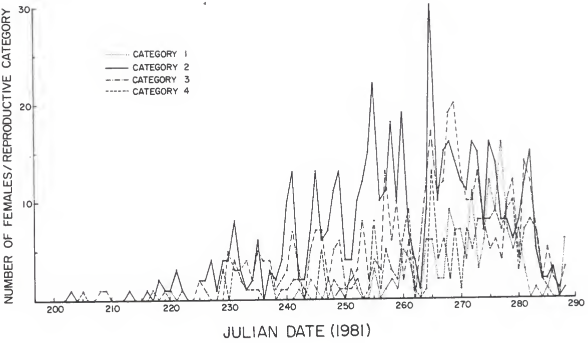

Figure 4.3. Total number of adult velvetbean caterpillar females per reproductive category per night. Categories are (1) unmated, no spermatophore, (2) mated, fat body content full to 1/3 depleted, (3) mated, fat body content 1/3 to 2/3 depleted, and (4) mated, fat body content 2/3 or more depleted. Females were caught in a blacklight trap during 1981 at the Green Acres Research Farm, Alachua County, FL.

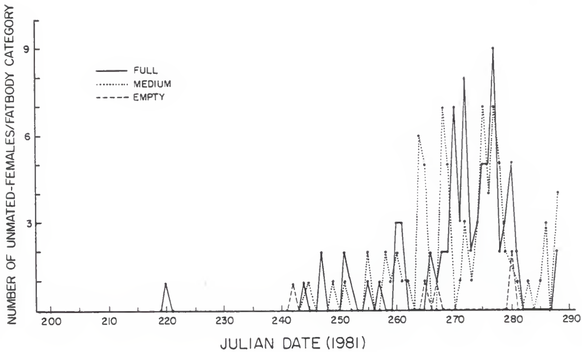

Figure 4.4. Total number of velvetbean caterpillar unmated adult females per fat body content category per night. Categories are full (fat body content full to 1/3 depleted), medium (fat body content 1/3 to 2/3 depleted) and empty (fat body content 2/3 or more depleted). Females were caught in a blacklight trap during 1981 at the Green Acres Research Farm, Alachua County, FL.

number of spermatophores per female (±SE) was 1.41 ± .019. Leppla (1976) found that colony females contained one to six spermatophores with a mean of 1.7 spermatophores per female. Wild females contained a smaller range of spermatophores but about the same mean.

The mean number of spermatophores per female per reproductive category (±SE) is listed in Table 4.3. All three categories of mated females exhibit a significantly different mean, indicating that the number of successful matings tended to increase with female age. The mean number of spermatophores per female per week varied between only one and two spermatophores (see Fig. 4.5), indicating that mating frequency was fairly constant over the field season and that most females mated at least once. The large confidence intervals at dates 203 and 210 are due to small sample size (n = 2 and 3, respectively).

Adult Trap-Cage

The mean number of VBC per 21.16 m^2 captured in the adult trap-cage during 1982 rose and fell steadily through the field season [see Fig. 4.6(A-C), and Appendix D, Tables D.4 and D.5 for raw data and mean values]. Initially, females were caught for two weeks before males were captured (Fig. 4.6). Perhaps females move into and reside in soybean before males. Densities of females and males, measured with the trap cage and BLT, peaked at ca. the same time (see Figs. 4.2 and 4.6). The mean densities of males and females from the trap cage peaked on date 246 - seven days before female density peaked in the BLT and four days after male density peaked in the BLT.

The capture of the first adults in the trap-cage (date 217, 5 August) corresponded with the closure of the soybean canopy; the canopy closed from late July to early August. No adults were caught with the trap-cage in the field prior to canopy closure but adults were caught in

Table 4.3. The mean number (±SE) of spermatophores per female per reproductive category of adult velvetbean caterpillar. Females were caught in a blacklight trap during 1981 at the Green Acres Research Farm, Alachua County, FL.

Reproductive Category[a]	Total Number of Females	Mean[b] Spermatophores/Female (±SE)
1	162	0
2	543	1.19 ± .02 A
3	376	1.40 ± .03 B
4	207	2.00 ± .05 C

[a] 1 = unmated, no spermatophore.
2 = mated, fat body content full to 1/3 depleted.
3 = mated, fat body content between 1/3 and 2/3 depleted.
4 = mated, fat body content 2/3 or more depleted.

[b] Means followed by different letters are significantly different according to the Kruskal-Wallis Test ($\alpha = .05$).

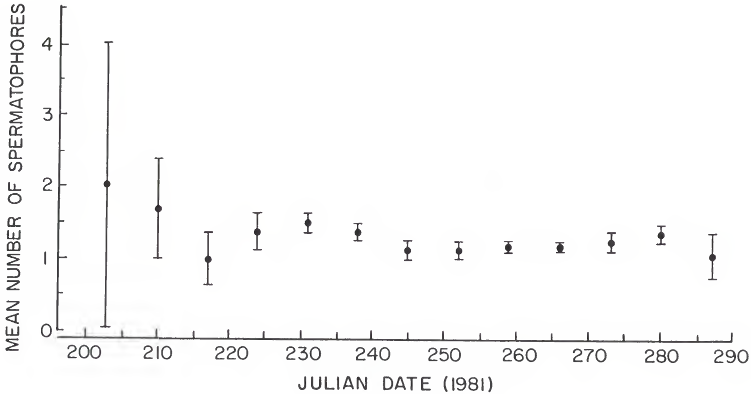

Figure 4.5. The mean number of spermatophores per adult velvetbean caterpillar female per week. Females were caught in a blacklight trap during 1981 at the Green Acres Research Farm, Alachua County, FL.

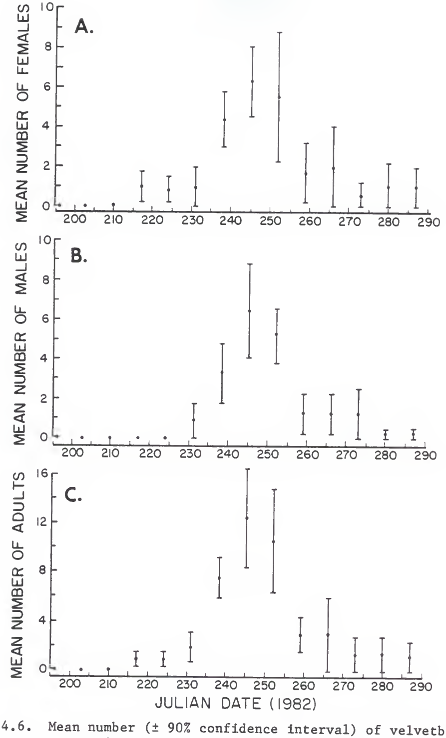

Figure 4.6. Mean number (± 90% confidence interval) of velvetbean caterpillar moths captured per sample (21.16 m^2) with the adult trap-cage: (A) females, (B) males, and (C) adults (females and males). Trap-cage was used in a 1 ha soybean field during 1982 at the Green Acres Research Farm, Alachua County, FL.

the BLT prior to canopy closure. From dates 190-216, 121 adults were caught in the BLT (see Fig. 4.2 and Appendix D, Table D.3). Based on BLT and trap-cage data, and on behavioral observations (see Chapter III), adults moved into the field at night but did not stay in the field during the day until the canopy began to close. Also, females laid eggs* in the field prior to being captured in the trap-cage. Adults may take-up "residence" in the field at canopy closure due to changes in atmospheric humidity or vapor pressure deficit.

Effect of Vapor Pressure Deficit

In 1981-82, ambient** vapor pressure deficit (VPD) was higher during the day [see Figs. 4.7(A) and 4.8(A)]. Field** VPD was high during the day until the canopy closed ca. 30 July '81 (date 211) and 27 July '82 (date 208)[see Figs. 4.7(B) and 4.8(B)]. In 1981, field VPD during the day fell below 5 mm Hg consistently after date 210 [see Fig. 4.7(B)]. Adults were first observed in the field on date 215. In 1982, field VPD during the day fell consistently below 5 mm Hg after date 207 [see Fig. 4.8(B)]. Adults were first observed in the field on date 214 and first captured in the trap-cage on date 217. In 1981 and 1982, adults moved into the field after the VPD had fallen below 5 mm Hg.

Late in the field season of 1982, as the soybean began to senesce and the VPD rose above 5 mm Hg, adults continued to be caught in the trap-cage. The reason for the continued presence of adults in soybean at this time is unclear but may have been due to physiological changes

*Eggs were first collected in samples on 5 July 1982, or date 186 (see Chapter V).

**Ambient and field VPD (day and night) are mean values based on readings of temperature and humidity that were recorded at 1 h intervals. See Appendix D, Table D.6, for formula used to calculate VPD.

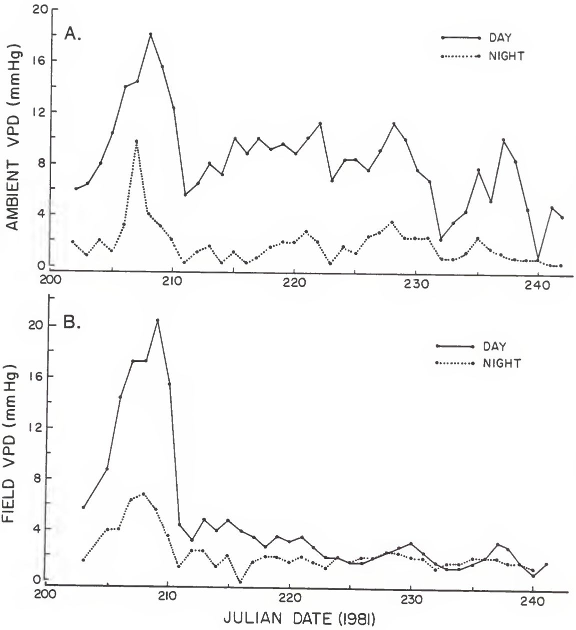

Figure 4.7. Vapor pressure deficit (VPD) in a 1 ha soybean field in 1981 at the Green Acres Research Farm, Alachua County, FL: (A) ambient VPD, and (B) field VPD.

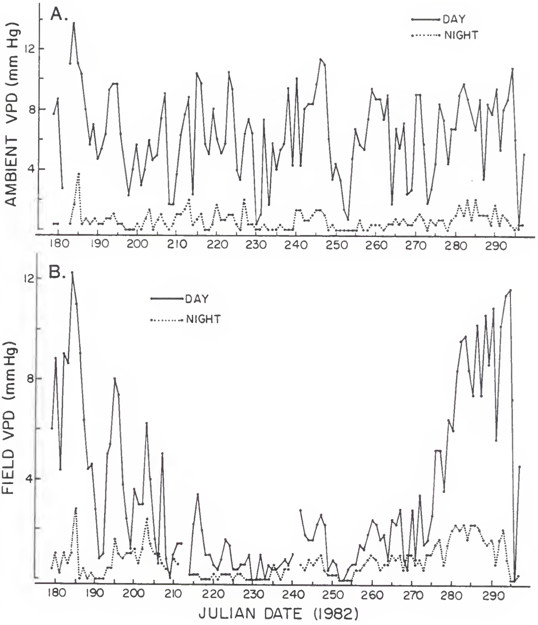

Figure 4.8. Vapor pressure deficit (VPD) in a 1 ha soybean field in 1982 at the Green Acres Research Farm, Alachua County, FL: (A) ambient VPD, and (B) field VPD.

within the moths; i.e., adults may have been more tolerant of higher VPD at this time of the year. Behavioral observations* tend to support this idea, as adults have been observed outside of soybean in areas of apparent dryness at this time of the year. The occurrence of VBC in these dry areas may be in response to the dry season that typically begins at this time in tropical areas. Adults appear to be well adapted for residing in dry leaf litter, as adults apparently are leaf mimics. The strong diagonal line across the wings may mimic a leaf main-vein. This diagonal line is maintained when the wings are held at rest. Other markings and patterns on the wings may represent various shadings of dried leaves and patches of lichens (see Figs. 3.1, 3.4, 3.6 and 3.7).

Sex Ratio

The sex ratio of adults caught in the BLT (per night) and the adult trap-cage (per week) are shown in Fig. 4.9; sex ratio is expressed as the number of males to total adults (Pianka 1978). The dashed line in each figure represents the seasonal mean sex ratio. The sex ratio of BLT adults was biased toward males for all three years but tended to show a decrease in bias as the season progressed (i.e., the sex ratios dropped below their mean values (see Fig. 4.9). The sex ratios for '80 and '82 are .54 and .51 (respectively) and are not significantly different, while the sex ratio in 1981 was much higher at .69 and is significantly different (see Table 4.4). Why the sex ratio for 1981 was so high is unknown. The sex ratio of the trap-cage adults is .35, is

*On 25 October 1981, 12 adults were observed at Osceola National Forest (Baker County, FL) in the grass and leaf litter of Sandhill and Pine Flatwood Communities. On 3 October 1982, 30 adults were observed at Cumberland Island (Camden County, GA) on dead oak leaves in the dry understory of a Maritime Community.

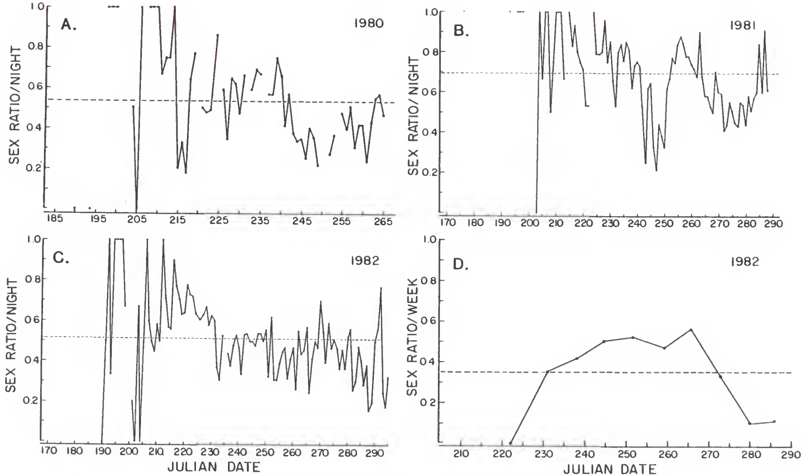

Figure 4.9. Sex ratio of velvetbean caterpillar adults caught in blacklight traps (BLT) and an adult trap-cage (ATC) in a 1 ha soybean field at the Green Acres Research Farm, Alachua County, FL: (A) 1980, BLT, (B) 1981, BLT, (C) 1982, BLT, and (D) 1982, ATC. Dashed line in all graphs represents the seasonal mean sex ratio.

Table 4.4. Mean seasonal sex ratios of adult velvetbean caterpillar caught in blacklight traps and an adult trap-cage in a 1 ha soybean field at the Green Acres Research Farm, Alachua County, FL.

Year	Trap[a]	Number of Samples	Mean Sex Ratio[b] (±SE)
1980	BLT	59	.54 ± .03 B
1981	BLT	89	.69 ± .02 C
1982	BLT	103	.51 ± .02 B
1982	ATC	49	.35 ± .05 A

[a]BLT = blacklight trap.
ATC = adult trap-cage.

[b]Means followed by different letters are significantly different according to Duncan's Multiple Range Test (α = .05).

distinctly biased toward females, and is significantly different from the other sex ratio values (see Table 4.4). Why this sex ratio is so low and biased toward females is unknown, but perhaps females prefer to reside in soybean while males prefer other sites.

Impact of Physical Variables

Select physical variables were regressed against BLT catch (1981-82) of females, males, and adults (females and males). Regression results with total BLT numbers are shown in Table 4.5. The parametric coefficient of flight temperature was significant in all of the models, except for females in 1982 (see Table D.6 for an explanation of flight temperature). The parametric coefficient of vapor pressure deficit was significant in three of the models, while the parametric coefficient of moonlight intensity was the only other coefficient to show significance. The effects of flight temperature and vapor pressure deficit on adult catch are understandable, as temperature (see Chapter III) and VPD (see Leppla 1976) affect VBC dynamics. The effect of moonlight intensity was unexpected as field observations (see Chapter III) had not disclosed such an affect; however, moonlight is known to affect the flight of many moths (see Nemec 1971, Bowden and Church 1973, Douthwaite 1978). Values of r^2 were much higher in 1981 than in 1982, but a large amount of variation in BLT response for both years was not explained.

Regression models for weighted BLT numbers are shown in Table 4.6. The predictive capabilities of these models are very poor, as reflected in their extremely low r^2 values. Low r^2 values for both total and weighted BLT models demonstrate that the proportion of total variation in the BLT responses, explained by the physical variables, is extremely low in most cases. Unknown and/or non-monitored environmental variables affected adult capture. Adult number may have varied due to area-wide

Table 4.5. Regression equations of physical variables[a] and total numbers of males, females, and adults of the velvetbean caterpillar. Moths were caught in a blacklight trap at the Green Acres Research Farm, Alachua County, FL. All parametric coefficients significant at $\alpha = .05$.

1981

$$\text{Female} = 39.18 - 3.15\ (\text{Temp}) + 6.46\ (\text{VPD}) - 24.03\ (\text{Moon})$$

$$(r^2 = .45)$$

$$\text{Male} = 75.91 - 4.73\ (\text{Temp})$$

$$(r^2 = .18)$$

$$\text{Adult} = 110.96 - 6.73\ (\text{Temp})$$

$$(r^2 = .23)$$

1982

$$\text{Female} = 37.82 - 11.04\ (\text{VPD})$$

$$(r^2 = .05)$$

$$\text{Male} = 9.63 + 2.26\ (\text{Temp})$$

$$(r^2 = .06)$$

$$\text{Adult} = 37.56 + 3.95\ (\text{Temp}) - 21.05\ (\text{VPD})$$

$$(r^2 = .10)$$

[a]Temp = temperature (°C).
VPD = vapor pressure deficit (mm Hg).
Moon = moonlight illuminence.

Table 4.6. Regression equations of physical variables[a] and weighted numbers of males, females, and adults of the velvetbean caterpillar. Moths were caught in a blacklight trap at the Green Acres Research Farm, Alachua County, FL. All parametric coefficients are significant at α = .05.

1981

$$\text{Female} = -16.74 - 0.25\ (\text{Moon}) + 0.02\ (\text{Baro})$$

$$(r^2 = .03)$$

$$\text{Male} = 0.58 - 0.003\ (\text{Windd})$$

$$(r^2 = .01)$$

Adult, no variables met the .05 significance level.

1982

$$\text{Female} = 24.66 - 0.14\ (\text{VPD}) + 2.94\ (\text{Rain}) - 0.02\ (\text{Baro})$$

$$(r^2 = .05)$$

$$\text{Male} = 0.17 - 0.24\ (\text{VPD}) + 0.26\ (\text{Moon}) + 3.34\ (\text{Rain})$$

$$(r^2 = .06)$$

$$\text{Adult} = 0.15 - 0.20\ (\text{VPD}) + 0.27\ (\text{Moon}) + 3.62\ (\text{Rain})$$

$$(r^2 = .06)$$

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[a]Moon = moonlight illuminence.
Baro = barometric pressure (MB).
Windd = wind direction.
VPD = vapor pressure deficit (mm Hg).
Rain = rainfall (cm).

20 ha) occurred in the general area of the study and supported populations of VBC.

Calibration of Adult Density

Linear regression was used to examine the relationship between the total number of moths captured in the BLT and the total number of moths in the field determined from trap-cage sampling data (see Appendix D, Table D.4). Significant relationships were found for females, males, and adults (females and males), although the proportion of the total variation, as explained by the BLT catch, is low for all three models (see Table 4.7). This low explanation is not surprising because BLT catch fluctuates nightly (see Fig. 4.2) and can not be predicted very well from weather variables (see Tables 4.5 and 4.6). Also, the models in Table 4.7 are not realistic biologically. Based on positive intercept values, these models demonstrate that moths are caught in the field before they are caught in the BLT. Sample data do not support this demonstration, as adults were caught in the BLT before they were caught in the field. Smoothing* the BLT data provides more realistic regression equations (i.e., negative intercepts) and increases r^2 ca. 20% (see Table 4.8).

Conclusions

This study represents the first quantitative assessment of adult VBC movement within a soybean field. Adult appearance (or density) in the field was measured with a blacklight trap (BLT) and coincided with the appearance of eggs, demonstrating that adult density can be monitored with a BLT and that a BLT is sensitive to adult capture at low

*Data were smoothed with a nonlinear data smoothing algorithm (3RSSH, twice) based on running medians (see Velleman 1980, Ryan et al. 1982).

Table 4.7. Regression equations of total daily number of velvetbean caterpillar moths in the field and total nightly number of moths caught in the blacklight trap during 1982 at the Green Acres Research Farm, Alachua County, FL. Total number of moths (females, males, and total adults) were determined with adult trap-cage data.

<u>Female</u>

$$FF = 134.11 + 23.20\ (FBLT),$$

where $r^2 = .26$
FF = total number of field females,
$FBLT$ = total number of BLT females.

<u>Male</u>

$$MF = 26.40 + 16.81\ (MBLT)$$

where $r^2 = .28$,
MF = total number of field males,
$MBLT$ = total number of BLT males.

<u>Adults</u>

$$AF = 129.25 + 20.20\ (ABLT)$$

where $r^2 = .32$,
AF = total number of field adults,
$ABLT$ = total number of BLT adults.

Table 4.8. Regression equations of total daily number of velvetbean caterpillar moths in the field and total nightly smoothed number of moths caught in the blacklight trap (BLT) during 1982 at the Green Acres Research Farm, Alachua County, FL. Total number of moths (females, males, and total adults) were determined with adult trap-cage data. BLT data were smoothed with a nonlinear data smoothing algorithm (3RSSH, twice) based on running medians (see Velleman 1980, Ryan et al. 1982).

Female

$$FF = -68.55 + 30.06\ (FBLT),$$

where $r^2 = .43$,
FF = total number of field females,
FBLT = smoothed number of BLT females.

Male

$$MF = -218.40 + 31.10\ (MBLT)$$

where $r^2 = .50$,
MF = total number of field males,
MBLT = smoothed number of BLT males.

Adult

$$AF = 340.74 + 31.66\ (ABLT)$$

where $r^2 = .55$,
AF = total number of field adults,
ABLT = smoothed number of BLT adults.

densities. Placement of the trap in the field was necessary to achieve this sensitivity. A number of physical variables were explored for their effect on BLT catch. No consistently adequate correlations among these variables and BLT catch were uncovered with regression techniques, suggesting that other variables might affect adult density fluctuations or that no simple linear relationships exist between these variables. Future experimental work should be directed toward determining the affect of various environmental variables on adult flight (e.g., wind speed). Quantitative descriptions of these affects in the form of mechanistic equations could be used to predict the capture of adults in blacklight traps. Dissections of adult females revealed that most females were found to be mated and potentially highly reproductive. Early in the field season, mated females flew into the field and contained large amounts of fat body, indicating that these females probably completed their larval development on nearby hosts.

Absolute estimates of adult absolute density were obtained with a unique sampling device, an adult trap-cage. Design and utilization of this trap resulted from adult behavioral observations (see Chapter III). Adult residency in the field during the day, as measured with this trap, appeared to be delayed until an appropriate humidity level (5 mm Hg) had been reached in the field during the day. Adult departure from the field, as soybean senesced, apparently was not affected by the same humidity level. To assess the true impact of humidity on VBC dynamics will require extensive experimentation in the field on a year-round basis in both soybean and other hosts, as well as the completion of detailed laboratory experiments.

Estimates of the relative and absolute densities of adults were calibrated with a regression equation. This equation could be used to

predict the number of adults in the field, given BLT catch. The number of adults in the field, as predicted by this equation, could be modified with mechanistic equations that describe the impact of environmental variables on adult capture in a blacklight trap. These mechanistic equations would exert their influence on the parametric coefficients of the regression equation. Overall, data that were critical to the construction of a model of adult and egg numbers of VBC were obtained (see Chapter VI): adult female density, female reproductive potential, and a calibration equation to convert BLT catch into field densities. Model completion required only one more piece of information, egg density data (see Chapter V).

CHAPTER V
MEASUREMENT OF EGG DENSITY

Introduction

Velvetbean caterpillar (VBC) larvae are a major defoliators of soybean in the Gulf Coast area of the United States (Herzog and Todd 1980). Adult VBC immigrate into soybean fields annually and pest problems result from oviposition by females and eclosion of larvae (see Ellisor 1942, Greene 1976, Herzog and Todd 1980, Buschman et al. 1981a, 1981b). As is the case for most pests, current management of VBC is directed at the symptoms of the pest problem (i.e., controlling larvae) and not the cause (i.e., sources of adults)(see Barfield and O'Neil 1984). Not surprisingly, virtually nothing is known about the timing and magnitude of adult movement or oviposition in soybean (see Rabb and Kennedy 1979, MacKenzie et al. 1985). Wilkerson et al. (1982) used a soybean/VBC dynamics model to describe how variation in the timing and magnitude of adults resulted in notable differences in soybean yield and grower profit (from -$289.63 to $178.43, see Table 1.1). Adult and egg densities used in the model were determined from estimated larval densities (Stimac,* personal communication). Examination of adult

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*J. L. Stimac, Associate Professor, Department of Entomology and Nematology, University of Florida, Gainesville, FL. 32611. Larval densities at time "t" were used to determine egg and adult densities at time "t-1" by calculating the densities of adults and eggs required to produce the known larval densities. Mortality values of adults and eggs were used in these calculations.

movement into soybean by quantifying adult and egg densities should provide better insight into the management of this pest.

Movement of VBC adults in a soybean field will be examined with a model of adult and egg populations in Chapter VI. Adult and egg density data were required for model construction. Adult density data are reported in Chapter IV and the present study is a report of egg density data.

Determination of egg density demanded the resolution of several methodological problems. First, confusion existed in the literature on the physical appearance of VBC eggs, particularly egg color (see Watson 1916a, Douglas 1930, Hinds 1930, Ellisor 1942, Greene et al. 1973, Gutierrez and Pulido 1978). Second, little was known about Lepidoptera eggs found on soybean plants (see Herzog and Todd 1980). Third, conflicting reports existed as to whether VBC eggs could be sampled (see Greene et al. 1973, Ferreira and Panizzi 1978). Lastly, egg and adult densities needed to be assessed simultaneously to describe the relationship between the two life stages, a formidable problem (see Oloumi-Sadeghi et al. 1975, Lopez et al. 1979, Buntin 1980, Hogg and Gutierrez 1980, Pedgley and Betts 1980).

Materials and Methods

Egg Development and Coloration

From 1980-84, VBC eggs from colony and wild adults were examined to determine their developmental times and coloration. Colony females were used in all years, except for wild females in 1983. Wild females were collected on 27 September 1983 with an aerial net in a 10 ha soybean field (cv. USV1) in Alachua County, FL. All females were maintained at 26.7° ± 1°C,

an individual oviposition cage and supplied with an ovipositional substrate of green paper* (see Moscardi 1979). Eggs were collected at 0.5 h after darkness by removal of the ovipositional substrate.

To determine temperature-dependent egg development, all collected eggs (from colony and wild adults) were maintained in growth chambers at a series of constant temperatures, 14L:10D photoperiod, and > 90% RH. In 1980-82, eggs were kept in Percival Growth Chambers (Model I-35LL) and, in 1983-84, in walk-in chambers (2.2 x 2.5 x 2.3 m). Egg development was studied at 4.0, 6.4, 10.4, 14.8, 19.5 and 26.7° ± 1°C (1980-81); at 23.9 and 26.7° ± 1°C (1982); at 26.7° ± 1°C (1983); and at 18.3, 21.1, 23.9, 26.7, 29.9, and 32.2° ± 1°C (1984). Egg coloration and development were monitored with a 70X dissecting microscope at variable time intervals (1980-81) and at hourly intervals (1982-84).

Field Sampling of Velvetbean Caterpillar Eggs

Eggs were sampled (1981-1982) twice a week in a 1 ha soybean field (cv. Bragg)** at the University of Florida's Green Acres Research Farm (ca. 22.5 km west of Gainesville, FL, Alachua County). Plants were selected with simple random allocation, cut at soil line, removed from the field and placed in a walk-in growth chamber (2° ± 1°C); plant stems were placed in water to delay leaf wilt. In 1981, 70 randomly selected plants were sampled on each sample date during the hour just before and after sunset***. Sample unit size equaled one plant. In 1982, 30 to

*Springhill Bond/Offset International Paper Co., color green, 10M weight, long grain.

**See Appendix A for agronomic practices and soybean phenological stages.

***Oviposition rate during these times is known to be extremely low (see Chapter III).

140 plants were sampled on each sample date between 0430 and 0630*. Sample unit size varied from one to two plants (see Appendix F for egg density data). Differences in sampling between 1981 and 1982 reflected knowledge gained on the temporal occurrence of oviposition (see Chapter III) and on temperature-dependent egg development. In all years, plants were removed individually from the walk-in chamber and all plant surfaces were searched for eggs. Typically, one to three days were required to search all the plants. Eggs were examined with a 70X dissecting microscope and identified to species (see Appendix E for an identification key of Lepidoptera eggs on soybeans). All VBC eggs were aged by coloration. On the first day of each sample date, all light-green VBC eggs were held and checked for viability. Eggs that speckled were considered viable (see below). Field temperature was monitored continuously at 0.2 m above ground with a hygrothermograph (Weather Measure Corp., Model H311).

Results and Discussion

Egg Development and Coloration

Velvetbean caterpillar eggs demonstrated a series of color changes during development that were temperature-dependent. "Freshly-laid" eggs typically were light green but also demonstrated off-white, transparent and faintly-green colors [Fig. 5.1(A)]. "Middle-aged" eggs were colored like freshly-laid eggs but were speckled brownish red; speckles also were brown, reddish brown and rarely white in color [Fig. 5.1(B)]. Eggs about to hatch were light brown, or "brownish", with a visible larval head-capsule [Fig. 5.1(C)].

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*Ovipositional rate during these times is known to be extremely low (see Chapter III).

A.

B.

C.

Figure 5.1. Eggs of the velvetbean caterpillar: (A) "freshly-laid" egg, light green in color, (B) "middle-aged" egg, light green in color with brownish-red speckles, and (C) "brownish" egg (i.e., about to hatch), light brown in color.

Mean development times (from 1982 data) for egg speckling, browning, and hatching were significantly different ($\alpha = 0.05$) between 23.9 and 26.7°C (Table 5.1). All eggs were light green when oviposited, but 15 failed to speckle (12 at 23.9°C and 3 at 26.7°C). All 15 of these eggs withered several days after oviposition and proved to be non-viable. All other eggs demonstrated the speckling pattern that persisted until browning. Thus, two vital components of the egg sampling plan were assessed: (1) the color morphs associated with egg development and (2) the temperature-dependency of egg development and color changes.

Eggs from wild females demonstrated the same color changes as those from colony females at 26.7°C (Fig. 5.1); however, wild eggs developed (and changed color) significantly faster ($\alpha = 0.05$)(Table 5.1). The reason for this result is unknown but could be an artifact of the small number of colony females that were examined (n = 3).

Mean development time and rate for speckling were determined (with 1984 data) at six different temperatures with eggs from colony adults (Table 5.2). Linear regression between developmental rate and temperature yielded the following equation:

$$y = -0.080430 + 0.006566(x),$$

where y = developmental rate of speckling, and

x = temperature (°C).

The coefficient of determination (r^2) was 0.90. Slope and intercept parameters were determined with all observations and not mean values. The developmental zero (DZ) for speckling was 12.25°C (Fig. 5.2), and the number of degree-hours required for speckling (thermal constant) was 153.27 (Table 5.2). Replacement of the developmental rate of colony

Table 5.1. Mean developmental time of speckled[a], brownish[b], and hatched[c] velvetbean caterpillar eggs at two different temperatures. Colony (1982) and wild (1983) females were used in the study.

Female Source	No. of Females	Temp. (°C)	Speckled Eggs[d] n	Speckled Eggs[d] $\bar{x} \pm SE$ (h)	Brownish Eggs[d] n	Brownish Eggs[d] $\bar{x} \pm SE$ (h)	Hatched Eggs[d] n	Hatched Eggs[d] $\bar{x} \pm SE$ (h)
Colony	4	23.9	73	18.9 ± .23A	67	106.8 ± .38D	65	117.2 ± .44G
Colony	3	26.7	65	13.3 ± .26B	65	60.7 ± .21E	61	67.1 ± .24H
Wild	10	26.7	166	9.5 ± .07C	158	59.1 ± .14F	157	64.0 ± .15I

[a] Speckled refers to an egg that is typically light green with brownish-red speckles.

[b] Brownish refers to an egg that is light brown with a visible head-capsule.

[c] Hatched refers to larval eclosion.

[d] Means followed by different letters are significantly different according to Kruskal-Wallis Test (α = .05).

Table 5.2. Mean developmental time and rate (±SE) for speckling to occur in VBC eggs from colony females at six different temperatures. Mean number of degree-hours required for speckling (thermal constant) was 153.27.

Temp. (°C)	Number of Females	Number of Eggs	Mean Development: Time (±SE) (h)	Mean Development: Rate (±SE) (1/h)	Degree-Hours
18.3	15	223	21.5 ± .09	.047 ± .0002	130.72
21.1	15	215	16.3 ± .07	.062 ± .0002	144.42
23.9	15	212	14.5 ± .10	.070 ± .0005	168.55
26.7	15	220	12.7 ± .09	.080 ± .0006	182.85
29.4	15	218	8.8 ± .05	.114 ± .0006	151.27
32.2	15	214	7.1 ± .02	.141 ± .0004	141.79

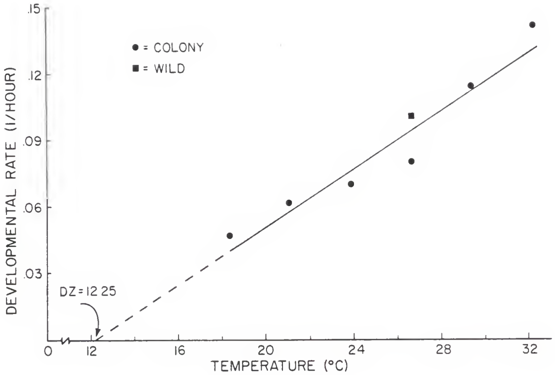


Figure 5.2. Developmental rate of speckling in VBC eggs at six different temperatures. Both colony and wild eggs were studied at 26.7°C. Developmental zero (DZ) for speckling was 12.25°C, and 153.27 degree-hours were required for speckling to occur. Mean estimates are shown in the figure for ease of view.

eggs at 26.7°C with the rate for wild eggs (see Table 5.1 and Fig. 5.2) yielded the following equation:

$$y = -0.082865 + 0.006826(x).$$

The coefficient of determination (r^2) was 0.94. Slope and intercept parameters were determined with all observations and not mean values. The slope of this equation does not differ significantly ($\alpha = 0.05$) from the slope of the previous equation, indicating that the difference in developmental rate between wild and colony eggs at 26.7°C does not significantly affect the relationship between temperature and egg developmental rate.

Field Sampling of Velvetbean Caterpillar Eggs

The thermal constant (153.27 degree-hours) was used to age eggs from field samples. Plants were removed from the field before degree-hour accumulation exceeded the thermal constant and were held for observation at 2°C (well below the DZ for egg development). The number of degree-hours accumulated between sunset (onset of oviposition) and plant sampling are listed in Table 5.3. In 1981, the accumulated degree-hours exceeded 153.27 on two dates (208 and 229) and were very close to the thermal constant on 7 of the remaining 13 sample dates (Table 5.3). With experience gained in 1981, plants were removed from the field in 1982 at an earlier time; consequently, most of the accumulated degree-hours were well below the thermal constant (Table 5.3).

At least two factors could have affected egg density estimates: (1) non-viable eggs and (2) egg mortality. All light-green eggs collected during the first day of sampling were examined for viability as indicated by the occurrence of speckling. All eggs speckled and hatched, indicating that females laid only viable eggs. The presence of

Table 5.3. The total number of degree-hours accumulated between sunset (onset of oviposition) and plant sampling during each sample date in 1981 and 1982. Mean number of degree-hours required for speckling to occur in VBC eggs is 153.27.

1981		1982	
Julian Date	Accumulated Degree-Hours	Julian Date	Accumulated Degree-Hours
204	124.1	186	96.4
208	161.3[a]	190	102.5
211	123.8	193	106.7
215	144.3	197	123.9
218	146.5	200	125.8
222	144.3	204	123.3
225	141.3	207	138.3
229	155.5[a]	211	131.1
232	140.8	214	144.3
236	143.8	218	93.6
239	140.3	221	118.3
243	128.4	225	112.6
246	132.8	228	117.6
250	113.8	232	107.5
257	11.5	235	125.8
		239	111.4
		242	105.2
		246	118.0
		249	107.9
		253	100.3
		256	110.5
		260	109.1
		263	116.4
		267	91.9
		270	75.0
		274	85.0
		277	118.9
		281	104.3
		284	115.0
		288	23.2

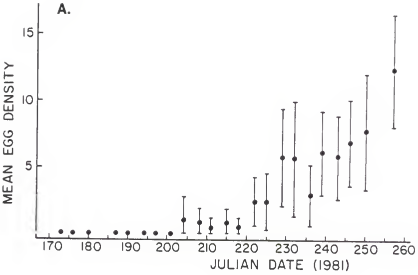
[a]Accumulated degree-hours exceeded 153.27.

non-viable eggs would have yielded inflated estimates of egg density (as both viable and non-viable eggs are initially the same color) and strongly biased adult-to-egg conversions in the oviposition model (see Chapter VI). With regard to mortality, previous studies (Elvin 1983) allowed for the assumption that mortality of freshly-laid eggs at night was minimal.

Mean densities of freshly-laid VBC eggs per .91 m-row in 1981 and 1982 are shown in Fig. 5.3. In 1981, egg density displayed a general rise from late July (date 204) to mid-September (date 257). In 1982, egg density demonstrated a general rise and fall through the season, with two exceptions: (1) unexplainable drops in density occurred on September 3 and 6 (dates 246 and 249), and (2) the wide confidence interval at date 264 resulted from sampling a plant with 78 eggs. Why there were so many eggs on this plant is unknown. Egg and adult densities in both years tended to change synchronously (see Chapter IV). Sample size, sample unit size, mean, and standard deviation of freshly-laid eggs for all sample dates are listed in Appendix F.

<u>Egg-Speckling Hypothesis</u>

Speckled VBC eggs may be colored cryptically as a result of the selective pressures of predators and parasites. Light-green eggs are easy to see on soybean, while speckled eggs are extremely difficult to see. Light-green eggs laid during early scotophase speckle just after sunrise and probably are difficult for predators to see. Light-green eggs laid during late scotophase are still light-green after sunrise and probably are easy for predators to see. Females that oviposit in early scotophase should demonstrate a higher reproduction fitness over females that lay eggs in late scotophase because (hypothetically) the sooner an egg is laid after sunset the greater its chances of survival from



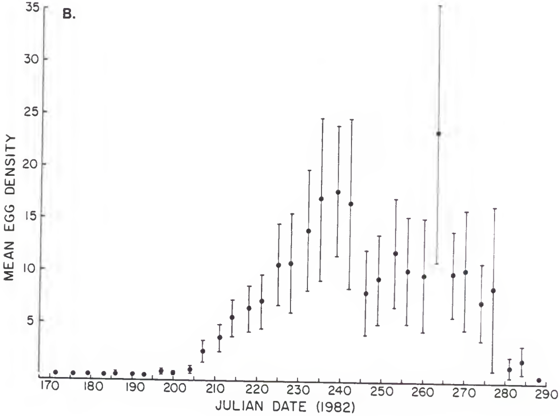


Figure 5.3. Mean densities per .91 m-row (± 95% confidence interval) of freshly-laid VBC eggs on soybean at the Green Acres Research Farm, Alachua County, FL: (A) 1981, and (B) 1982.

predation. Evidence supporting this hypothesis can be found in Gregory (see Chapter III), Greene et al. (1973), and Wales (1983), all of whom found that the majority of oviposition occurs in the early hours of scotophase.

Conclusions

Velvetbean caterpillar eggs are polychromatic, which accounts for the wide variation of color descriptions found in the literature. Color changes associated with egg development are temperature-dependent and can be used to age eggs and to determine when to sample for eggs. Eggs can be sampled readily, but care must be taken as to the time of egg sampling if eggs are to be aged. Typically, three days will be required to collect and process any given egg sample. Also, controlled environmental facilities (for holding plants and eggs at cool temperatures) are required to "suspend" egg development. The number of VBC eggs deposited on any given night can be determined using the methods presented in this study. These methods might be useful also in studies of other moth species (e.g., *Heliothis* spp.) with polychromatic eggs. Estimates of egg density (per night) would have been impossible without knowledge of the temporal occurrence of oviposition (see Chapter III). Collection of egg density data represented the final experimental data needed for model construction. These data were essential for comparison between model predictions and field estimates (see Chapter VI).

CHAPTER VI
A MODEL OF VELVETBEAN CATERPILLAR ADULT AND EGG POPULATIONS

Introduction

Crop/plant models can be used "to simulate the dynamics of a crop and pests in a single field so that decisions can be made regarding pest management and other production practices for that field" (Stimac and O'Neil 1985, p. 323). One such crop/pest model is the Soybean Integrated Crop Management (SICM) model (Wilkerson et al. 1982, 1983). This model is composed of an aggregate of submodels that describe the physiology of soybean growth in the presence or absence of abiotic and biotic stresses. The model is designed to allow the user to study various crop production and pest management strategies at the field level for different weather patterns, cultural practices, and insect pest scenarios.

One of the SICM submodels represents the population dynamics of velvetbean caterpillar (VBC), a major defoliating pest of soybean (Herzog and Todd 1980, Wilkerson et al. in press). Simulations with SICM and the VBC submodel demonstrate that changes in the pattern (timing and magnitude) of adult VBC influx and subsequent oviposition, result in dramatic differences in soybean yield and net profit (see Table 1.1). Adult and egg densities in the model were determined from estimated larval densities. Larval densities at time "t" were used to determine egg and adult densities at time "t-1" by calculating the adult and egg densities required to produce the measured larval densities at

time "t"; field estimated mortality values for eggs were used in the calculations. No direct estimates of adult and egg densities existed prior to the present study. Knowledge of adult influx patterns and ovipositional capacities within soybean fields is necessary to be able to adequately model VBC dynamics in soybean. The goal of the present study is to describe the relationship between VBC adult and egg densities in soybean and to construct a model that simulates changes in VBC egg density.

Model Objective

The model objective is to mimic VBC egg density in a soybean field. The behavioral criterion of this objective is to simulate changes in the density of VBC eggs in .91 m-row of soybean within the 95% confidence intervals of field estimates. Field estimates of egg density were made twice-a-week. Inputs into the model include (1) the number of adult females caught in a blacklight trap, (2) soybean field size, and (3) soybean phenological stage.

Data Requirements for Model Construction and Validation

Model construction and validation are based on data collected at the Insect Population Dynamics Laboratory (1980-84) of the University of Florida, and at the Green Acres Research Farm (1980-82) near Gainesville, FL. At the farm, data were collected in a 1 ha soybean field (cv. Bragg, see Appendix A for agronomic details and soybean phenological stages). The temporal resolution of the model is daily but model output is compared to field data taken at twice-a-week intervals. The spatial resolution of the model is a soybean field and is set by specifying the number of rows and row length in the soybean field.

Daily temporal resolution was selected so that the number of females caught on a particular night in the blacklight trap could be

"compared" with the number of eggs laid during that same night and because the VBC submodel in the SICM model operates on a daily resolution. Construction on the same temporal and spatial resolution as the VBC submodel was necessary if the adult egg population model is to be incorporated into the dynamics model. Sampling and manpower constraints restricted the estimation of field egg density to twice-a-week intervals. Consequently, model predictions of egg density are compared to field estimates at twice-a-week intervals. Data required for model structure, determination of parameters, comparison of model behavior, and validation were acquired from the completion of nine separate experiments in the following areas:

(1) adult identification (see Appendix B),
(2) observation of adult behavior in the field (see Chapter III),
(3) relative estimates of adult density (see Chapter IV),
(4) absolute estimates of adult density (see Chapter IV),
(5) female reproductive states (see Chapter IV),
(6) egg identification (see Appendix E),
(7) egg developmental rate (see Chapter V),
(8) absolute estimates of egg density (see Chapter V), and
(9) monitoring of various environmental variables (see Chapters III, IV, and V).

Sampling for adults would have been impossible without proper adult identification. Behavioral observations of adults in the field revealed temporal patterns in flight and oviposition. Knowledge of these patterns was necessary for the development of adult and egg sampling methodologies and for the acquisition of adult and egg density

estimates. Relative and absolute estimates of adult densities were collected in 1981 and 1982 and were used for model construction, parameterization, and model validation. Dissection data of adult females indicated that the majority of females in the field were potentially highly reproductive. These data were used to estimate the proportion of mated females in the field. Proper identification of VBC eggs and knowledge of egg developmental rate stipulated explicitly the temporal occurrence of egg sampling and allowed for the determination of absolute density estimates of freshly-laid eggs in the field (see Chapter V). Freshly-laid eggs were one day old or less.

Model Assumptions

Model assumptions are listed below:

(1) There is a linear relationship between the total number of females captured in the blacklight trap and the total number of females in the field.

(2) All females are able to mate.

(3) There is no mortality of mated females prior to oviposition.

(4) There is no mortality of eggs during the first day after oviposition.

(5) Ovipositional rate is the same for all females.

(6) Ovipositional rate is influenced by soybean phenological stage.

(7) Site-specific environmental conditions do not influence capture of adults in the blacklight trap.

Model Conceptualization

A conceptual model of adult and egg dynamics is shown in Fig. 6.1. A series of state variables are represented by acronyms shown in boxes in Fig. 6.1. The state variables represent the numbers of individuals

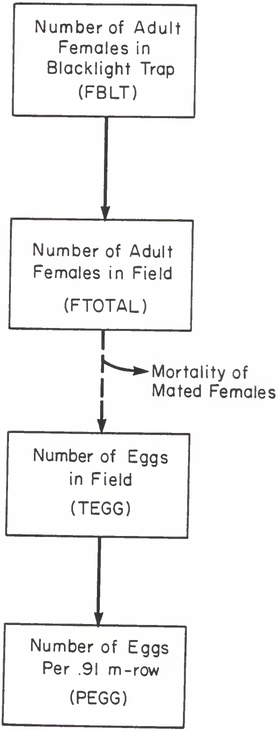


Figure 6.1. Flow diagram of a model of VBC adult and egg populations in a soybean field. See the text for an interpretation of this diagram.

of a particular VBC stage that occur within a soybean field over any given 24 h period. Arrows between boxes represent the flow of individuals from one state variable to the next. During each time step of the model, the total number of females captured in the blacklight trap (FBLT) is converted to the total number of females in the field (FTOTAL); all females are assumed to be mated. After female mortality has been imposed, total egg density (TEGG) is calculated by multiplying the total number of females and ovipositional rate. The "broken-line" arrow between FTOTAL and TEGG indicates that the transfer of numbers between the state variables is not an additive process but a multiplicative process. A conversion function (PEGG) is used to predict mean egg density per .91 m-row of soybean.

Model Structure

The model was written in SAS,* which provides tools for information storage and retrieval, data modification, programming, report writing, statistical analysis, and file handling. The SAS program and data files are listed in Appendix G. SAS was operated at the University of Florida on an IBM 3090, Model 200. Model output is discrete and model functions are deterministic. Functions used in the model are concerned with (1) the conversion of the total number of females captured in the BLT into the number of females in the field, (2) the total number of mated females in the field, (3) female mortality, (4) the total number of eggs laid per female, (5) the total number of eggs laid in the field, and (6) the predicted mean number of eggs per .91 m-row of soybean. Each of these functions are described below.

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*SAS User's Guide: Basics, and SAS User's Guide: Statistics, can be obtained from SAS Institute Inc., P. O. Box 8000, Cary, North Carolina, 27511-8000, 919/467-8000.

Function for Total Female Population

The total number of females captured in the blacklight trap is converted into the field density of females based on the following linear regression equation:

$$FTOTAL = 134.11 + 23.20\ (FBLT),$$

where FTOTAL is the total number of females in the field, FBLT is the total number of females captured in the blacklight trap, and 134.11 and 23.20 are the intercept and slope coefficients estimated from linear least squares. The parameters were estimated using data collected during 1982 at the Green Acres Research Farm (see Chapter IV for details on data collection and analysis).

Functions for Mated Female Population and Mortality

Mated female population (M_F) is determined with the following function:

$$M_F = (FTOTAL)(1-V_F)(1-MORT),$$

where FTOTAL is the total number of females in the field, V_F is the proportion of virgin females in the population and MORT is the proportional mortality of mated females per night. The quantity $(1-V_F)$ is the proportion of mated females and the quantity (1-MORT) is the proportional survival of mated females.

In the current version of the model, values for V_F and MORT are assumed to be zero. There are several reasons why these variables are set to values of zero. First, both can act in a compensatory fashion in the present model form. Secondly, data on the number of virgin females in the population are available only for 1981. These data values are near zero during most of the field season. Thirdly, there are no data on mortality estimates of adult females in the field. The current model version has been used to identify these data deficiencies.

Functions for Oviposition

Ovipositional rate (OVI) is represented in two ways: (1) by a constant, and (2) by a variable. OVI is the total number of eggs oviposited per female per night in the field. In the first function, OVI is set at a constant value of 220. This value yielded more adequate model behavior than other constant values (see below). Also, this value was less than the highest ovipositional rate reported in the literature (see Olivera 1981). In the second function, OVI is variable:

$$OVI = \begin{cases} 0 \text{ if } & 1 \leq SOY \leq 5 \\ 40 \text{ if } & 5 < SOY \leq 9 \\ 220 \text{ if } & 9 < SOY \leq 14 \\ 80 \text{ if } & 14 < SOY \leq 15 \\ 210 \text{ if } & 15 < SOY \leq 17 \\ 60 \text{ if } & 17 < SOY \leq 19 \\ 0 \text{ if } & 19 < SOY \leq 20, \end{cases}$$

where SOY represents the soybean phenological stage. Values of SOY were determined by modifying the soybean phenological system developed by Fehr and Caviness (1977)(see Table 6.1). Values of OVI for a given SOY value were determined with model simulations using 1982 field data and thus include the effects of all unknown variables, in addition to the "true" phenology effect Increases in vegetative growth from V1 to V9 were assigned sequentially increasing SOY values from 1 to 9. The V-stage prior to flowering (V10 in 1982) and the first reproductive stages (R1, R2) were assigned the same SOY value. The remaining R-stages were assigned sequentially increasing SOY values, except for the R5 and R6 stages. Both of these stages lasted considerably longer

Table 6.1. Parametric values of ovipositional rate and SOY used in the oviposition function of the adult and egg population model of velvetbean caterpillar. Values are based on data collected in 1982 and model simulations.

Length of[a] Soybean Stage (Days)	Soybean[b] Phenological Stage	SOY Value[c]	Oviposition[d] Rate
-	VE, VC	1	0
4	V1	1	0
4	V2	2	0
4	V3	3	0
3	V4	4	0
7	V5	5	0
4	V6	6	40
3	V7	7	40
4	V8	8	40
-	V9	9	40
4	V10	11	220
7	R1, R2	11	220
11	R3	12	220
3	R4	13	220
7	Early R5	14	220
18	Mid R5	15	80
10	Late R5	16	210
7	Early R6	17	210
10	Late R6	18	60
3	R7	19	60
1	R8	20	0

[a] A hyphen means that the corresponding soybean phenological stage must have occurred but was not observed in the field.

[b] See Fehr and Caviness (1977) or Tables 2.1 and 2.2 for a complete description of these stages. In the stage descriptions "V" refers to vegetative and "R" refers to reproductive.

[c] Values of the parameter SOY were based on modifications of the Fehr and Caviness (1977) system for determination of soybean phenological stage. See the text for a discussion of SOY values.

[d] Ovipositional rate is the total number of eggs oviposited per female per night on soybean.

than the other stages (35 and 18 days, respectively) and were partitioned into separate SOY values.

The linkage expressed between ovipositional rate and soybean phenology in the OVI function constrains the model to give predicted egg density values only if soybean is available. This linkage allows for interaction between VBC and soybean. Biological justification, or support, for the oviposition values in this function are discussed below in the model behavior section. Use of the OVI function requires that soybean phenological stage be converted into SOY values for each simulated data set.

<u>Function for Total Egg Number</u>

The total number of eggs in the field (TEGG) is represented by the function:

$$TEGG = (M_F)(OVI),$$

where M_F and OVI are the same as described earlier.

<u>Function for Predicted Egg Density</u>

The predicted mean number of eggs laid per .91 m-row of soybean (PEGG) is represented by the function:

$$PEGG = TEGG/ROW,$$

where TEGG equals the total number of eggs laid in the field and ROW equals the total number of .91 m-row of soybean in the field.

Model Behavior

Although all models are an abstraction of reality, their behavior should be consistent with observations made on the real system (Stimac 1977, Overton 1977). Desired model behavior can be specified explicitly in the behavioral criteria of a model objective. The degree to which a model meets these behavioral criteria dictates how well model

performance is validated against the real system (Stimac 1977, Overton 1977).

The model objective of the present study is to mimic VBC egg nightly density in a soybean field. The behavioral criterion of this objective is to simulate densities of VBC eggs per .91 m-row of soybean within 95% confidence intervals of field estimates made at twice-a-week intervals. The model inputs are (1) adult female density from a blacklight trap, (2) field size, and (3) soybean phenological stage. The goal of the present behavioral analysis is to obtain desired model behavior with 1982 egg density data (i.e., mimic field estimates of egg density) and to validate model behavior against the 1981 field estimates of egg density. Several simulations were conducted to accomplish this goal.

Simulation of 1982 Egg Population with a Constant Ovipositional Rate

Initial simulations with the model were made with constant nightly ovipositional rates that did not exceed rates reported in the literature (see Moscardi et al. 1981b, 1981c, Olivera 1981, Olivera et al. 1984). A rate of 220 eggs per female per night yielded the most appropriate model behavior, but this behavior was deemed inadequate as only 12 of 34 predicted values fell within the 95% confidence intervals of the estimated field densities (see Fig. 6.2). The upper and lower values of the confidence intervals are represented in Fig. 6.2 as hypens. Predicted values tended to fall outside of the confidence intervals in groups, indicating that a variable ovipositional rate might provide more adequate behavior.

Simulation of 1982 Egg Population with a Variable Ovipositional Rate

Model behavior was explored with an ovipositional rate that varied with soybean phenological stage. Model behavior was deemed adequate

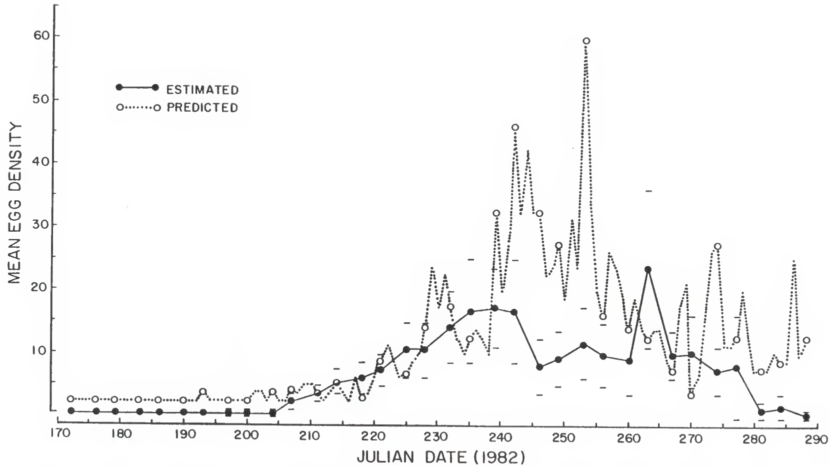

Figure 6.2. Mean velvetbean caterpillar egg density per .91 m-row of soybean during 1982 in a 1 ha field at the Green Acres Research Farm, Alachua County, FL. Estimated density with 95% confidence intervals determined from field collected data. Upper and lower values of the confidence intervals are represented as hypens. Predicted density determined with model simulations. Ovipositional rate was a constant during the simulation.

with this function because 31 of 34 predicted values fell within the 95% confidence intervals of the estimated field densities for 1982 data (see Fig. 6.3). The three predicted values that fell outside the confidence intervals occurred on dates when blacklight trap catch numbers were two to nine times higher or lower than "expected". A five-day moving average was used to determine "expected" blacklight trap catch values*. Use of the "expected" values placed predicted egg densities within their respective 95% confidence intervals. Why the number of captured females was higher or lower than expected is unknown. Frequent daily fluctuations in predicted egg density during the field season (see Fig. 6.3) were caused by numerical fluctuations in BLT catch, as all other variables were held constant (or changed slowly) in the model.

The rationale for determining the variable ovipositional rate is specified as follows. Ovipositional rate was set equal to zero during the early stages of soybean growth (VE to V5) when adult and egg densities were zero or very low. Based on field data, females were in the area of the soybean field during early soybean growth but were not ovipositing in the field (see Chapter IV). As soybean grew vegetatively (V6 to V9), adult and egg densities increased and ovipositional rate was set to a value of 40 eggs per female per night. From approximately soybean flowering (V10) to beginning pod maturity (early R6), a high ovipositional rate (OVI = 220 or 210) provided adequate model behavior except for an 18 day period when ovipositional rate had to be reduced to 80 eggs per female per night. Evidently, from flowering to early pod

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*A five-day moving average is calculated by determing the mean of five days: the date of interest and the two days before and after the date of interest. Expected values were 5.2 (date 218), 77.8 (date 253), and 26.4 (date 270).

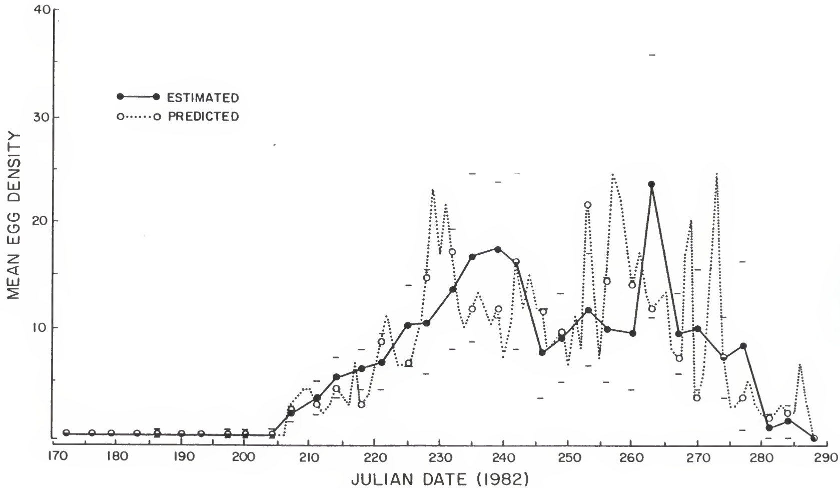

Figure 6.3. Mean velvetbean caterpillar egg density per .91 m-row of soybean during 1982 in a 1 ha field at the Green Acres Research Farm, Alachua County, FL. Estimated density with 95% confidence intervals determined from field collected data. Upper and lower values of the confidence intervals are represented as hyphens. Predicted density determined with model simulations. Ovipositional rate was variable during the simulation.

maturity, females "preferred" to lay large numbers of eggs on soybean, with the one exception already mentioned. During late pod maturity, soybean began to senescence and adult and egg densities declined. Presumably, females found soybean less attractive for oviposition at this time; consequently, ovipositional rate was set to 60 eggs per female per night. At full pod maturity (R8) when most foliage had senesced, eggs were not present in the field, so the ovipositional rate was set equal to zero. Females apparently will not oviposit on senescent soybean foliage, which is to their selective advantage as eclosed larvae would die for lack of suitable host plant material.

The reason for the necessary decline in ovipositional rate from 220 to 80 eggs per female per night during SOY 15 (or R5) is unknown but at least two explanations are plausible. Perhaps the adult-density conversion function acts inappropriately at SOY 15 (or R5). This seems unlikely as the function works well in simulations with data from 1981 (see below). Perhaps females altered their ovipositional rate in response to an environmental variable. A high daily vapor pressure deficit (VPD) in the field from dates 240-248 may have been the environmental factor that affected ovipositional rate in the field and led to the calculated value of 80 eggs per female per night [see Fig. 4.7(B)]. One might anticipate that future model versions use the rate of 210 or 220 eggs per female per night from R1 to R6, or use a function that varies ovipositional rate with VPD.

Why or if ovipositional rate in the field varies throughout the season in response to soybean phenological stage (as depicted in the model) is unknown. If it does occur, it may be induced by changes in leaf area, in VPD, in biochemical changes in the soybean, or by changes in VBC demographics. A great diversity of stimuli are known to

influence the behavior of ovipositing insects (see Hinton 1981). "Among species that do not practice any form of parental care following egg deposition, proper egg placement is particularly crucial. In the final stages of site selection considerable time and energy may be spent on fine discriminations regarding a wide variety of factors related to food availability, food suitability, and predator pressures." (Matthews and Matthews 1978, p. 404). For example, adult females of the noctuid moth Autographa precationis (Guenee) prefer to oviposit on soybeans over dandelions apparently because soybean leaf shape is a more effective oviposition stimulus; however, larvae demonstrate a marked feeding preference for dandelions (Kogan 1975). In another example, Heliconius butterflies in the Neotropics spend considerable time inspecting host plants prior to oviposition, apparently searching for Heliconius eggs or larvae because larvae are cannibilistic (Gilbert 1975). Finally, pipevine swallowtail butterflies, Battus philenor (Linnaeus), select host plants largely in response to leaf shape cues (Papaj and Rausher 1983).

Simulation of 1981 Egg Population with a Variable Ovipositional Rate

Quantitative validation of model behavior was attempted by comparing simulated egg density with 1981 field estimates. Ovipositional rates and other parameters were determined with experimental data and model simulations from 1982. Data specific to 1981 (i.e., soybean phenological stage and field size) were incorporated into the 1981 model structure. Simulations depicted in Fig. 6.4, show that 15 of 23 (65%) predicted egg density values fell within 95% confidence intervals of field estimates. The six disagreements between predicted and estimated values from dates 197 to 218 indicate that

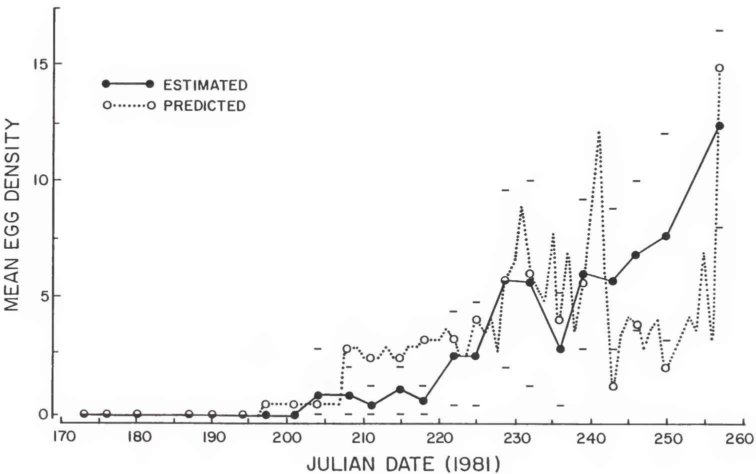

Figure 6.4. Mean velvetbean caterpillar egg density per .91 m-row of soybean during 1981 in a 1 ha field at the Green Acres Research Farm, Alachua County, FL. Estimated density with 95% confidence intervals determined from field collected data. Upper and lower values of the confidence intervals are represented as hyphens. Predicted density determined with model simulations. Ovipositional rate was variable during the simulation.

oviposition was depressed early in the 1981 season. Why is unknown, but rainfall in early 1981 was very low and retarded soybean growth (see Appendix A and Table 4.2). Perhaps VBC ovipositional rate was altered in response to poor soybean growth or high VPD which would occur in a drought-stressed crop. Field VPD in the day was very high during dates 200–210 and dropped below 4 mm Hg by date 216 [see Fig. 4.6(B)].

The two disagreements between predicted and estimated values at dates 243 and 250 reflect a general depression in predicted egg density from dates 243 to 256 (or R5). This depression resulted from an ovipositional rate of 80 eggs per female per night as determined from 1982 model simulations. Replacement of this rate with 200 eggs per female per night yields more acceptable behavior. Evidently, something depressed ovipositional rate in the field during R5 in 1982 but not in 1981.

Conclusions

Addition of the adult and egg population model into the VBC dynamics model would make the dynamics model more realistic. Equations that describe adult and egg numbers in the current dynamics model are based on relationships that were determined with estimated larval densities. Therefore, changes in larval density are based on assumed changes in adult influx. If larval densities are actually sensitive to adult influx then changes in adult influx must be demonstrated with experimental data and equations must be written that are based on these data. These equations would add more realism to the dynamics model.

Differences in model behavior between 1981 and 1982 indicate that structural modifications with the model would be needed to achieve more

desirable model behavior. These modifications could be made with any or all of the following functions: (1) total female number, (2) mated female number, (3) mated female mortality, and (4) ovipositional rate. Those functions that describe total female number and ovipositional rate would appear to be the most important functions to modify, as simulations revealed that the model was sensitive to changes in the values of these functions. Experimental evidence of a variable ovipositional rate should be gathered and quantified, particularly with reference to VPD. Also, further examination of the function that describes total female number may reveal that the mathematical description of this function could be described more adequately with a mechanistic representation. Collection of additional adult density estimates with the BLT and the adult trap-cage would provide a more complete data base for determination of the mathematical form of this function and for determination of what variables might affect this function. Use of a constant or a function to describe the proportion of mated females and mated female mortality, based on field collected data, might provide more adequate model behavior.

The present model has limited applicability as it is a site-specific model based on two years of data; however, incorporation of this model into the VBC dynamics model would allow for larval densities to be predicted with BLT catch. Ultimately, the prediction of larval densities with BLT catch could be used to eliminate scouting for larvae in fields until adult populations reach some predetermined density. The acquisition of additional data on adult and egg numbers from different years would allow for model analysis, improvements and refinements. Overall, the establishment of the quantitative relationship between

adult and egg populations with the current model represents an accomplishment that many researches have aspired for but have not obtained.

CHAPTER VII
SUMMARY AND CONCLUSIONS

Simulations with the Soybean Integrated Crop Management (SICM) model (and its VBC dynamics submodel) served as both a guide and template for present studies. These simulations indicated that changes in the pattern of adult VBC influx (i.e., timing and magnitude) resulted in dramatic differences in soybean yield and profit (see Table 1.1). Adult and egg numbers used in these simulations were determined from estimated larval densities, as data on numbers of adults and eggs were not available. Consequently, equations that describe adult and egg numbers in the current VBC dynamics model are based on assumed relationships. Replacement of these equations with others based on field collected data would probably add more realism to the dynamics model and allow for the ability to predict economically damaging larval densities with the use of adult density data.

The present study was conducted to estimate and model populations of VBC adults and eggs. The objective of this model was to mimic VBC egg densities in a soybean field within 95% confidence intervals of estimated means. To accomplish this objective, experiments were conducted to understand or quantify the following:

(1) adult moth identification (see Appendix B),

(2) adult behavior in the field (see Chapter III),

(3) relative estimates of adult density (see Chapter IV),

(4) absolute estimates of adult density (see Chapter IV),

(5) female reproductive states (see Chapter IV),

(6) egg identification (see Appendix E),

(7) egg developmental rates (see Chapter V),

(8) absolute estimates of egg density (see Chapter V), and

(9) the impact of various environmental variables on adult and egg dynamics (see Chapters III, IV, and V).

Summary and conclusion sections for each of these experiments are presented in respective chapters; Appendices B and E contain appropriate discussion sections. These sections will not be repeated here in their entirety, but important results will be discussed and highlighted in respective order.

Adult VBC are similar in morphological appearance to another noctuid moth, Mocis latipes Guenee. Differences and similarities between these two species are presented in Appendix B and should be useful information to researchers encountering both (e.g., both are caught in blacklight traps). Proper identification of VBC adults was necessary in the present study for acquisition of data on VBC adult numbers.

The role of the behavioral ecology study in the present work cannot be overemphasized. Observations of adult behavior were quantified and revealed temporal patterns in flight, mating, oviposition, and feeding. Flight occurred primarily at night. During the day, adults resided in the field but only after the soybean canopy had begun to close or was closed. During the day adults flew only when disturbed or rarely if feeding. Approximately 96% of all oviposition occurred within the first six hours of scotophase.

Knowledge of the temporal occurrence of adult flight and residency in the field allowed for the development of a unique adult sampling

methodology (an adult trap-cage) and the acquisition of adult density data. Model construction and validation required these adult density data. Knowledge of the temporal occurrence of oviposition allowed for the development of a unique egg sampling methodology, the determination of egg age and the acquisition of egg density data. Egg density was determined for eggs that were less than 24 h old because model construction and validation required data on the number of eggs oviposited in the field on a particular night.

Estimates of adult density were obtained with a blacklight trap (relative density) at nightly intervals and an adult trap-cage (absolute density) at weekly intervals. These estimates represented the first quantitative assessment of adult dynamics within a soybean field. Adult appearance (or density) in the field, as measured with a blacklight trap (BLT), coincided with the appearance of eggs and demonstrated that adult density can be monitored with a BLT and that a BLT is sensitive to adult capture at low densities. Placement of the BLT in the field was necessary to achieve this sensitivity. Dissection of adult females caught in the BLT in 1981 revealed that most females during the season were mated and potentially highly reproductive. Early in the field season, mated females that flew into the field contained large amounts of fat body, indicating that these females probably completed their larval development on nearby hosts. In the model, all females were mated and had reproductive rates that did not exceed literature-reported values.

Select physical variables were explored with multiple linear regression for their effect on blacklight trap catch. No consistently adequate correlations among these variables and BLT catch were uncovered, suggesting that there are no simple linear relationships

among these variables. Use of correlation techniques may be inadequate for predicting changes in VBC adult trap catch. A mechanistic model may be required for the prediction of these changes.

The adult trap-cage provided data on the absolute density of adults that was not obtainable with other techniques. An adult flushing technique* was tried in 1980 but was considered inadequate because adults of VBC and _M. latipes_ could not be identified separately while in flight. Based on data obtained with the trap cage, females established residency in the field before males, as both sexes were caught in the BLT prior to female residency. Adult residency appeared to be delayed until an appropriate humidity level (5 mm Hg) had been reached in the field during the day. Adult departure from the field, as soybean senesced, apparently was not affected by the same humidity level. To assess the true impact of humidity on VBC dynamics will require extensive experimentation in the field on a year-round basis in both soybean and other hosts, as well as the completion of detailed laboratory experiments.

Relative and absolute estimates of adult density were calibrated with a linear regression equation. This equation was used in the model structure to predict the number of adults in the field based on BLT catch. In its present form, the calibration equation is static because it changes value only if BLT catch changes. Values of this equation could be modified by mechanistic equations that describe the impact of environmental variables on adult capture in a blacklight trap (e.g., the effect of wind speed on adult flight).

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*See Pedigo (1980) for a discussion of this sampling method.

Velvetbean caterpillar eggs are similar in morphological appearance to a number of other lepidopteran eggs found on soybean. Differences and similarities among these eggs are discussed in Appendix E and should be useful information to researchers encountering these eggs. Accurate identification of VBC eggs is necessary to sample and measure egg density.

Velvetbean caterpillar eggs are polychromatic and change color during development. The appearance of these different colors is temperature-dependent and was used to age eggs. Determination of the mean number of eggs oviposited per 0.91 m-row in soybean per night was possible only after the acquisition of knowledge on the temporal occurrence of oviposition and the establishment of a sampling time based on the temperature-dependent color changes of eggs. This approach avoided the problem of indiscriminately partitioning VBC eggs into various age categories as model construction and validation required data on the number of eggs oviposited in the field on a particular night. Egg density data collected in 1982 were necessary for model construction and determination of parametric values, while egg density data from 1981 served for model validation.

Egg densities predicted by the model were more accurate with a variable ovipositional rate as opposed to a constant rate. The variable ovipositional rate was linked to changes in soybean phenology and allowed for interaction between VBC and soybean. In model validation, 65% of the model's predicted values fell within the 95% confidence intervals of the 1981 field estimates. Differences between predicted and estimated values were attributed to unpredictable fluctuations in BLT catch and to variation in ovipositional rate between years. The

variations in ovipositional rate appeared to be related to higher than normal canopy VPD caused by drought periods.

Differences in model behavior between 1981 and 1982 indicated that structural modifications in the model should produce more desirable model behavior. Model behavior should be improved by writing mechanistic equations that account for fluctuations in BLT catch and variation in ovipositional rate. Attainment of these mechanistic equations will depend on the collection of additional data on adult and egg numbers and on identification and quantification of those environmental variables that affect BLT catch and oviposition. For example, wind tunnel tests could be used to quantify the impact of wind speed on adult flight. Also, experimental evidence of a variable ovipositional rate should be acquired and quantified.

The adult and egg population model developed in this study should be incorporated into the VBC dynamics model, as equations that describe adult influx in the dynamics model are not based on field collected adult density estimates. Determination of the robustness of the population model awaits the collection of additional data on adult and egg numbers and an evaluation of the model's behavior with these data. These data should be collected at numerous sites to examine variation in the effect of site specific environmental conditions. Also, an analysis of model behavior with the model as part of the overall dynamics model should be completed.

Overall, the present study has provided the framework, manifested as a model, necessary to measure the intra-field dynamics of a noctuid moth. This framework can serve as template for other researchers who seek to develop a quantitative relationship between adult and egg

populations. In the past, numerous researchers have attempted unsuccessfully to establish such a relationship.

APPENDIX A

AGRONOMIC PRACTICES AND SOYBEAN PHENOLOGICAL-STAGES

Table A.1. Agronomic practices from 1980-1982 in a soybean field at Green Acres Research Farm, Alachua County, FL.

Description	Year		
	1980	1981	1982
Field Size (ha)	.88	.82	.87
Number of Rows	112	102	110
Row Length (m)	103.35	107.00	103.66
Previous Winter Cover Crop	Unknown	Rye Grass	Rye Grass & Lupine
Pre-Plant Herbicide (ml/ha)	585, Surflan	585, Treflan	1169, Treflan
	877, Lexone	877, Sencor	877, Lexone
Muriate of Potash (kg/ha)	258	111	104
Planting Date	June 3	June 12	June 9
Soybean Variety	Bragg	Bragg	Bragg
Row Spacing (m)	.76	.76	.76
No. of Plants/.91 row-m, Sample Date	10, June 3	28.267, July 24	12.733, August 9

Table A.1 (continued)

Cultivation	July 9, Sweeps	July 13, Sweeps	July 14, Rolling
		July 23, Rolling	July 21, Rolling
Irrigation	June 4, 5 cm	June 12, 5 cm	June 9, 1.3 cm
		July 29, 5 cm	
Harvest Date	October 17	October 14	October 22
Seed Moisture (%)	10.7	13	10.7
Yield (kg/ha)	901.1	1303.6	2030.3

Table A.2. Soybean phenological stages in an ca. 1 ha field in 1981 at the Green Acres Research Farm, Alachua County, FL; phenological stages were not determined in 1980. Sample size was 70 plants per sample date. Plants were staged according to the methods of Fehr and Caviness (1977).

Calender Date	Julian Date	Vegetative Stage	Reproductive Stage
June 22	173	VC	-
25	176	V1	-
29	180	V2	-
July 6	187	V3	-
9	190	V4	-
13	194	V5	-
16	197	V6	-
20	201	V7	-
23	204	V7	-
27	208	V8	-
30	211	V9	R1, R2
Aug. 3	215	V10	R2
6	218	V11	R2
10	222	V12	R3
13	225	V13	R3
17	229	V13	R3
20	232	V13	R4
24	236	V13	R5
27	239	V13	R5
31	243	V13	R5
Sept. 3	246	V13	R5
7	250	V13	R5
14	257	V13	R5
21	264	V13	R6
29	272	V13	R7
Oct. 4	277	V13	R8
13	286	V13	R8

Table A.3. Soybean phenological stages in an ca. 1 ha field in 1982 at the Green Acres Research Farm, Alachua County, FL; phenological stages were not determined in 1980. Sample size varied from 30 to 70 plants, dependent upon sample date. Plants were staged according to the methods of Fehr and Caviness (1977).

Calender Date	Julian Date	Vegetative Stage	Reproductive Stage
June 21	172	V1	-
25	176	V1	-
28	179	V2	-
July 2	183	V3	-
5	186	V4	-
9	190	V5	-
12	193	V5	-
16	197	V6	-
19	200	V7	-
23	204	V8	-
26	207	V10	-
30	211	V11	R1, R2
Aug. 2	214	V12	R1, R2
6	218	V13	R3
9	221	V13	R3
13	225	V13	R3
16	228	V14	R4
20	232	V14	R5
23	235	V14	R5
27	239	V14	R5
30	242	V14	R5
Sept. 3	246	V14	R5
6	249	V14	R5
10	253	V14	R5
13	256	V14	R5
17	260	V14	R5

Table A.3 (continued)

Calender Date	Julian Date	Vegetative Stage	Reproductive Stage
Sept. 20	263	V14	R5
24	267	V14	R6
27	270	V14	R6
Oct. 1	274	V14	R6
4	277	V14	R6
8	281	V14	R6
11	284	V14	R7
15	288	V14	R8

APPENDIX B

IDENTIFICATION OF ADULT *Anticarsia gemmatalis* Hubner AND *Mocis latipes* (Guenee)

Anticarsia gemmatalis Hubner

Wing Span

35-40 mm (Forbes 1954).

Dorsal Wing Surface

Forewing and hindwing: Basic wing coloration is extremely variable and ranges from ashen gray to light yellowish-brown to reddish-brown (Watson 1916a, Forbes 1954, Kimball 1965, Leppla et al. 1977). Wing pattern is mottled and shaded, and wing-mark colorations are highly variable and include black, white, gray, brown, and ochre [Fig. B.1(A and C)].

Forewing: The postmedial line is distinctive and runs obliquely from the wing apex to the approximate middle of the anal margin [Fig. B.1(A and C), letter a]. The reniform spot on each forewing is large, irregular, pale, and usually faint (sometimes obscure)[Fig. B.1(A and C), letter b].

Hindwing: The postmedial line is distinctive and runs essentially parallel to the outer margin [Fig. B.1(A and C), letter c].

Postmedial line: The postmedial line is distinctive and runs obliquely from the apex of the forewing to the approximate middle of the anal margin of the hindwing [Fig. B.1(A and C), letters a and c].

Ventral Wing Surface

Forewing and hindwing: Wing color is light brown or cinnamon brown (Watson 1916a). Wing pattern is shaded and wing-mark colorations are restricted to various shades of brown and white. The subterminal line

is a series of white dots that run parallel to the outer wing-margin [Fig. B.1(B and D), letter d].

Sexual Dimorphism

Males have tufts of long setae that are present on the femora of prothoracic legs and the tibiae of the metathoracic legs [Fig. B.1(B), letter e]. These long setae are absent on female legs [Fig. B.1(D)] (Anonymous 1974).

Mocis latipes (Guenee)

Wing Span

35-40 mm (Forbes 1954).

Dorsal Wing Surface

Forewing: Wing coloration is light gray, light brown, or dull brownish-red (Hampson 1913, Forbes 1954). Wing pattern is shaded, and wing-mark colorations are brown, gray, and grayish-brown [Fig. B.2(A and C)]. The postmedial line is nearly parallel to the outer wing-margin and is essentially straight, except for a slight bend just below the costa [Fig. B.2(A and C), letter a]. The reniform spot is generally evident, vaguely circular, and usually touches the subreinform spot [Fig. B.2(A and C), letter b]. The subreniform spot is usually distinct, usually circular, and may open onto the postmedial line [Fig. B.2(A and C), letter c]. When viewed at the same time, the reniform and subreniform spot resemble a figure eight [Fig. B.2(A and C), letters b and c].

Hindwing: Wing coloration is light gray, light brown, or grayish-brown [Fig. B.2(A and C)](Hampson 1913 and Forbes 1954). In general, wing marks are vague or absent. The postmedial line is usually present, usually vague, and nearly parallel to the outer wing-margin [Fig. B.2(A and C), letter d].

Postmedial line: The postmedial line of the forewing and the hindwing form a line (sometimes vague) that parallels the outer wing-margins [Fig. B.2(A and C), letters a and d].

Ventral Wing Surface

Forewing and hindwing: Wing color is light brown or light gray and wing marks are vague or absent, except for the terminal line [Fig. B.2(B and D)].

Sexual Dimorphism

Males have tufts of long setae that are present on the tibiae and tarsi of the metathoracic legs [Fig. B.2(B), letter e]. The long setae of the metathoracic legs can be easily seen. Long setae are absent on female legs [Fig. B.2(D)](see Bethune 1869, Gundlach 1881, and Wolcott 1948).

Differences Between *A. gemmatalis* and *M. latipes*

The main difference between the dorsal wing surface of *A. gemmatalis* and *M. latipes* is the placement of the postmedial line. On *A. gemmatalis* the postmedial line runs obliquely from the forewing apex to the approximate middle of the anal margin of the hindwing [Fig. B.1(A and C, letters a and c]. On *M. latipes* the postmedial line of the forewing and hindwing form a line (sometimes vague) that parallels the outer wing-margin [Fig. B.2(A and C), letters a and d].

The main difference between the ventral wing surfaces of the two species is the development of the subterminal line. On *A. gemmatalis*, the subterminal line is a series of white dots that run parallel to the outer wing-margin [Fig. B.1(B and D), letter d]. On *M. latipes*, the subterminal line is very vague, or not present. If present, the line is not a series of white dots [Fig. B.2(B and D)].

Differences in leg scales of the two species are evident. On male A. gemmatalis, tufts of long setae occur only on the tibiae of metathoracic legs [Fig. B.1(B), letter e]. On male M. latipes, tufts of long setae on the metathoracic legs occur on the tibiae and the tarsi [Fig. B.2(B), letter e].

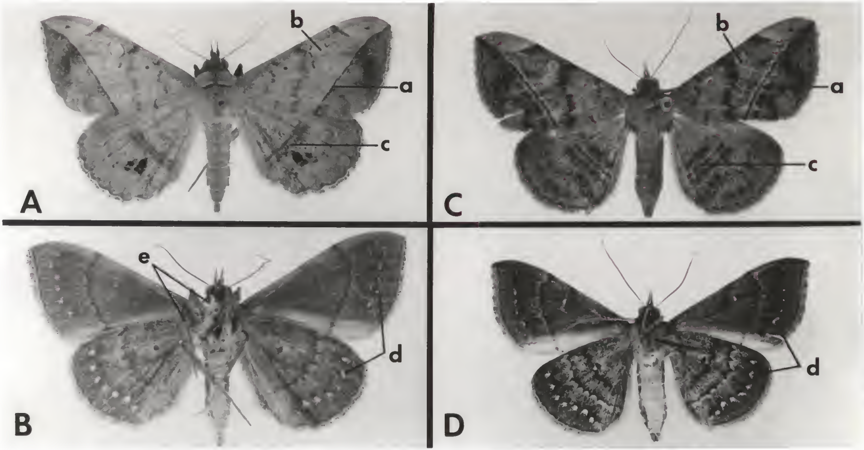

Figure B.1. View of adult Anticarsia gemmatalis Hubner, the velvetbean caterpillar: (A) male, dorsal view, (B) male, ventral view, (C) female, dorsal view and (D) female, ventral view. Legend: a = postmedial line, b = reniform spot, c = postmedial line, d = subterminal line, e = long setae on male legs. Adults collected by G. Strickland: male, 24 September 1969, East Baton Rouge Parish, LA; female, 3 October 1970, East Baton Rouge Parish, LA. Both specimens are on deposit at the Florida State Collection of Arthropods, Gainesville, FL.

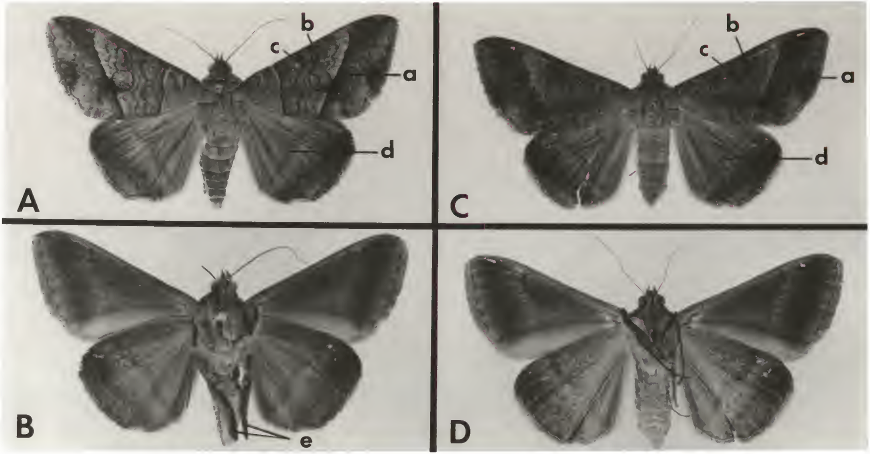

Figure B.2. View of adult Mocis latipes (Guenee), striped grass looper: (A) male, dorsal view, (B) male, ventral view, (C) female, dorsal view, and (D) female, ventral view. Legend: a = postmedial line, b = reniform spot, c = subreniform spot, d = postmedial line, e = long setae on male legs. Adults collected by Tom Dean (ex ova labrotorio): male and female, 31 October 1984, Alachua County, Gainesville, FL. Both specimens are on deposit at the Florida State Collection of Arthropods, Gainesville, FL.

APPENDIX C

BEHAVIORAL OBSERVATIONS: QUANTITATIVE TECHNIQUE AND DATA

A detailed explanation and an example of the quantitative technique, for analysis of observational data on oviposition, mating, and feeding, are presented. Data in Tables C.1 and C.2 are artificial for ease of discussion. In Table C.1, data are presented on number of observations, observation times, and weighted observations. The observational time of hour 1 is 30 min, and the number of observations of the activity is 1. The weighted observation for hour 1 is .03; one observation divided by 30 min equals .03. Six observations occur during hours 2 and 3. Based on the number of observations for hours 2 and 3, the activity is equally prevalent during each hour. This equality is misleading because 60 min were required to make the observations in hour 2, while 30 min were required in hour 3; i.e., twice as much time was spent in hour 2 to see the same number of observations. The weighted observations for hours 2 and 3 are .10 and .20, respectively. The value for hour 3 is twice as large as the value for hour 2. The difference between the weighted values for the two hours properly reflects the differences in observational time between the two hours.

In Table C.2, data are presented on weighted observations, sample means, normalized means, and percent normalized means. Data are grouped by hour after sunset, irregardless of year, month, and day. For hour 1, the sample mean of the weighted observations is determined as follows: $.03 + .01 + .02 = .06/3 = .02$. The sum of the sample means for all 12 hours is .82. Each sample mean is normalized by division with .82. The normalized sample means add up to the value of one. A percent normalized sample mean is obtained by multiplying the appropriate normalized sample mean by 100.

Table C.1. Artificial data of an adult activity and the technique for determination of the temporal frequency of that activity during scotophase -- calculation of the weighted observations for a particular day.

Hour After Sunset	Number of Observations	Observational Time (min)	Weighted[a] Observations (obs./min)
1	1	30	.03
2	6	60	.10
3	6	30	.20
4	2	60	.03
5	1	60	.02
6	0	0	.00
7	0	0	.00
8	0	0	.00
9	0	60	.00
10	0	45	.00
11	0	45	.00
12	0	30	.00

[a] $\text{Weighted Observations} = \frac{\text{Number of Observations}}{\text{Observational Time}}$

Table C.2. Artificial data of an adult activity and the technique for determination of the temporal frequency of that activity during scotophase -- calculation of sample means, normalized means, and percent normalized means with weighted observations. Different years, months, and nights have been combined.

Hour After Sunset	Date[a] (D-M-Y)	Weighted[b] Observation	Sample[c] Mean	Normalized[d] Mean	Percent[e] Mean
1	27-A-80	.03	.02	.0244	2.44
	07-S-80	.01			
	20-A-81	.02			
2	27-A-80	.10	.15	.1829	18.29
	20-A-81	.10			
	14-S-82	.20			
	21-S-82				
3	21-A-81	.25	.25	.3049	30.49
	29-A-81	.30			
	24-S-81	.25			
	25-S-81	.20			
4	17-S-81	.14	.16	.1951	19.51
	10-S-82	.18			
5	23-A-81	.11	.14	.1707	17.07
	17-S-81	.17			
6	23-A-81	.05	.06	.0732	7.32
	13-S-81	.07			
	04-S-82	.06			
7	13-S-81	.01	.02	.0244	2.44
	04-S-82	.01			
	25-S-82	.04			
8	13-S-81	.00	.01	.0122	1.22
	25-S-81	.02			
	13-S-81	.01			
9	13-S-81	.00	.00	.0000	0.00
	24-A-82	.00			
	28-A-82	.00			
10	21-A-81	.02	.01	.0122	1.22
	25-A-81	.00			

Table C.2 (continued)

Hour After Sunset	Date[a] (D-M-Y)	Weighted[b] Observation	Sample[c] Mean	Normalized[d] Mean	Percent[e] Mean
11	28-A-81	.00	.00	.0000	0.00
	01-S-81	.00			
	04-S-81	.00			
	08-S-81	.00			
	13-S-81	.00			
12	25-A-81	.00	.00	.0000	0.00
	28-A-81	.00			
		Total	.82	1.0000	100.00

[a]D-M-Y = Day, Month, Year; A = August, S = September; 80 = 1980, 81 = 1981, 82 = 1982.

[b]For calculation of individual weighted observations see Table C.1.

[c]Sample mean of weighted observations for each hour; e.g., for first hour after sunset, sample mean = .02 = (.03 + .01 + .02)/3.

[d]Normalized Mean = Sample Mean/.82.

[e]Percent Mean = Normalized Mean x 100.

Table C.3. Observation data on mating of adult velvetbean caterpillar in a 1 ha soybean field at Green Acres Research Farm, Alachua County, FL, 1980-82. Weighted observations are also given.

Date[a] (D-M-Y)	Hour After Sunset	Number of[b] Observations of Mating	Observational[c] Time (min)	Weighted[d] Observations
05-A-80	1	0	49	0.000000
15-A-81	1	1	60	0.016667
19-A-81	1	0	60	0.000000
22-A-81	1	1	60	0.016667
26-A-81	1	0	60	0.000000
29-A-81	1	2	35	0.057143
02-S-81	1	0	60	0.000000
05-S-81	1	0	59	0.000000
09-S-81	1	1	49	0.020408
12-S-81	1	0	60	0.000000
17-S-81	1	1	60	0.016667
19-S-81	1	1	50	0.020000
24-S-81	1	0	60	0.000000
26-A-82	1	0	40	0.000000
03-S-82	1	3	10	0.300000
24-S-82	1	0	60	0.000000
05-A-80	2	1	60	0.016667
15-A-81	2	1	60	0.016667
19-A-81	2	0	39	0.000000
22-A-81	2	2	60	0.033333
26-A-81	2	0	30	0.000000
29-A-81	2	2	35	0.057143
02-S-81	2	1	60	0.016667
05-S-81	2	0	3	0.000000
09-S-81	2	12	28	0.428571
12-S-81	2	1	21	0.047619
17-S-81	2	4	60	0.066667

Table C.3 (continued)

Date[a] (D-M-Y)	Hour After Sunset	Number of[b] Observations of Mating	Observational[c] Time (min)	Weighted[d] Observations
19-S-81	2	0	60	0.000000
24-S-81	2	1	60	0.016667
26-A-81	2	5	60	0.083333
03-S-81	2	15	60	0.250000
24-S-81	2	0	45	0.000000
05-A-80	3	4	60	0.066667
15-A-81	3	2	35	0.057143
22-A-81	3	2	32	0.062500
26-A-81	3	1	60	0.016667
29-A-81	3	2	40	0.050000
02-S-81	3	1	15	0.066667
09-S-81	3	10	42	0.238095
12-S-81	3	4	49	0.081633
17-S-81	3	4	60	0.066667
19-S-81	3	1	18	0.055556
24-S-81	3	0	37	0.000000
26-A-82	3	0	18	0.000000
03-S-82	3	11	40	0.275000
10-S-82	3	1	38	0.026316
24-S-82	3	0	50	0.000000
05-A-80	4	1	11	0.090909
15-A-81	4	2	50	0.040000
16-A-81	4	0	10	0.000000
22-A-81	4	0	45	0.000000
23-A-81	4	0	3	0.000000
26-A-81	4	1	36	0.027778
29-A-81	4	1	35	0.028571
09-S-81	4	5	38	0.131579
12-S-81	4	2	60	0.033333

Table C.3 (continued)

Date[a] (D-M-Y)	Hour After Sunset	Number of[b] Observations of Mating	Observational[c] Time (min)	Weighted[d] Observations
17-S-81	4	5	45	0.111111
19-S-81	4	3	45	0.066667
03-S-82	4	14	60	0.233333
10-S-82	4	2	60	0.033333
24-S-82	4	9	60	0.150000
16-A-81	5	0	35	0.000000
23-A-81	5	0	60	0.000000
27-A-81	5	0	33	0.000000
12-S-81	5	0	21	0.000000
17-S-81	5	0	28	0.000000
03-S-82	5	0	11	0.000000
04-S-82	5	1	19	0.052632
10-S-82	5	0	19	0.000000
24-S-82	5	1	37	0.027027
25-S-82	5	0	18	0.000000
16-A-81	6	0	55	0.000000
23-A-81	6	0	42	0.000000
13-S-81	6	2	44	0.045455
04-S-82	6	1	60	0.016667
25-S-82	6	4	60	0.066667
16-A-81	7	0	30	0.000000
13-S-81	7	1	21	0.047619
04-S-82	7	0	11	0.000000
25-S-82	7	0	3	0.000000
16-A-81	8	0	60	0.000000
13-S-81	8	0	39	0.000000
25-S-81	8	1	33	0.030303
16-A-81	9	0	60	0.000000
13-S-81	9	0	60	0.000000

Table C.3 (continued)

Date[a] (D-M-Y)	Hour After Sunset	Number of[b] Observations of Mating	Observational[c] Time (min)	Weighted[d] Observations
28-A-82	9	0	27	0.000000
31-A-82	9	0	24	0.000000
04-S-82	9	0	19	0.000000
07-S-82	9	0	1	0.000000
11-S-82	9	0	11	0.000000
14-S-82	9	0	7	0.000000
18-S-82	9	0	2	0.000000
25-S-82	9	1	52	0.019231
16-A-81	10	0	45	0.000000
18-A-81	10	0	23	0.000000
21-A-81	10	0	20	0.000000
25-A-81	10	0	16	0.000000
28-A-81	10	0	13	0.000000
01-S-81	10	0	8	0.000000
04-S-81	10	0	4	0.000000
13-S-81	10	0	60	0.000000
28-A-82	10	0	53	0.000000
31-A-82	10	1	60	0.016667
04-S-82	10	0	51	0.000000
07-S-82	10	0	59	0.000000
11-S-82	10	0	59	0.000000
14-S-82	10	0	60	0.000000
18-S-82	10	0	60	0.000000
21-S-82	10	0	58	0.000000
25-S-82	10	0	53	0.000000
16-A-81	11	0	48	0.000000
18-A-81	11	0	51	0.000000
21-A-81	11	0	56	0.000000
25-A-81	11	0	60	0.000000

Table C.3 (continued)

Date[a] (D-M-Y)	Hour After Sunset	Number of[b] Observations of Mating	Observational[c] Time (min)	Weighted[d] Observations
28-A-81	11	0	60	0.000000
01-S-81	11	0	60	0.000000
04-S-81	11	0	60	0.000000
08-S-81	11	0	60	0.000000
13-S-81	11	0	6	0.000000
15-S-81	11	0	51	0.000000
31-A-82	11	1	36	0.027778
14-S-82	11	0	8	0.000000
18-S-82	11	0	23	0.000000
21-S-82	11	0	17	0.000000
25-S-82	11	0	32	0.000000
25-A-81	12	0	2	0.000000
28-A-81	12	0	7	0.000000
01-S-81	12	0	14	0.000000
04-S-81	12	0	19	0.000000
08-S-81	12	0	25	0.000000
15-S-81	12	0	38	0.000000

[a]D-M-Y = Day, Month, Year; A = August, S = September; 80 = 1980, 81 = 1981, 82 = 1982.

[b]Total number of observations of mating was 157.

[c]Total number of observational minutes was 5162.

[d]Weighted Observations = $\frac{\text{Number of Observations}}{\text{Observational Time}}$

Table C.4. Sample mean and standard error of the weighted observations of mating velvetbean caterpillar adults are grouped by post-sunset hour, along with the percent normalized sample mean and standard error. Observations were made from 1980-82 at the Green Acres Research Farm, Alachua County, FL, in a 1 ha soybean field.

Hour After Sunset	n[a]	Sample Mean of the Weighted Observations (±SE)	Percent Normalized[b] Sample Mean (±SE)
1	16	.0280 ± .0185	9.60 ± 6.36
2	16	.0646 ± .0288	22.15 ± 9.87
3	15	.0709 ± .0208	24.31 ± 7.13
4	14	.0676 ± .0183	23.19 ± 6.27
5	10	.0080 ± .0056	2.73 ± 1.94
6	5	.0258 ± .0132	8.84 ± 4.52
7	4	.0119 ± .0119	4.08 ± 4.08
8	3	.0101 ± .0101	3.46 ± 3.46
9	10	.0019 ± .0019	.66 ± .66
10	17	.0009 ± .0010	.34 ± .34
11	15	.0019 ± .0019	.64 ± .64
12	6	.0000 ± .0000	.00 ± .00

[a] n = number of weighted observations per sample mean; n is not the number of mating observations. See Table C.3 for complete listing of all observations and observational times.

[b] Percent normalized sample mean = (sample mean of weighted observations/0.291516)*100. Percent normalized sample mean = (standard error of sample mean/0.291516)*100.

Table C.5. Observational data on oviposition by adult velvetbean caterpillar females in a 1 ha soybean field at the Green Acres Research Farm, Alachua County, FL, 1981-82. Weighted observations are also given.

Date[a] (D-M-Y)	Hour After Sunset	Number of[b] Observations of Oviposition	Observational[c] Time (min)	Weighted[d] Observations
19-A-81	1	2	60	0.033333
22-A-81	1	3	60	0.050000
26-A-81	1	1	60	0.016667
29-A-81	1	1	35	0.028571
02-S-81	1	1	60	0.016667
05-S-81	1	2	59	0.033898
09-S-81	1	0	49	0.000000
12-S-81	1	1	60	0.016667
17-S-81	1	9	60	0.150000
19-S-81	1	10	50	0.200000
24-S-81	1	0	60	0.000000
26-A-81	1	0	40	0.000000
03-S-81	1	1	10	0.100000
24-S-81	1	10	60	0.166667
19-A-81	2	1	39	0.025641
22-A-81	2	0	60	0.000000
26-A-81	2	0	30	0.000000
29-A-81	2	3	35	0.085714
02-S-81	2	1	60	0.016667
05-S-81	2	0	3	0.000000
09-S-81	2	0	28	0.000000
12-S-81	2	2	21	0.095238
17-S-81	2	2	60	0.033333
19-S-81	2	2	60	0.033333
24-S-81	2	1	60	0.016667
26-A-82	2	9	60	0.150000

Table C.5 (continued)

Date[a] (D-M-Y)	Hour After Sunset	Number of[b] Observations of Oviposition	Observational[c] Time (min)	Weighted[d] Observations
03-S-82	2	7	60	0.116667
24-S-82	2	5	45	0.111111
22-A-81	3	0	32	0.000000
26-A-81	3	0	60	0.000000
29-A-81	3	0	40	0.000000
02-S-81	3	0	15	0.000000
09-S-81	3	0	42	0.000000
12-S-81	3	2	49	0.040816
17-S-81	3	3	60	0.050000
24-S-81	3	0	37	0.000000
26-A-81	3	0	18	0.000000
03-S-81	3	6	40	0.150000
10-S-81	3	0	38	0.000000
24-S-81	3	6	50	0.120000
22-A-81	4	0	45	0.000000
23-A-81	4	0	3	0.000000
26-A-81	4	0	36	0.000000
29-A-81	4	0	35	0.000000
09-S-81	4	0	38	0.000000
12-S-81	4	0	60	0.000000
17-S-81	4	1	45	0.022222
03-S-82	4	8	60	0.133333
10-S-82	4	4	60	0.066667
24-S-82	4	5	60	0.083333
23-A-81	5	0	60	0.000000
27-A-81	5	0	33	0.000000
12-S-81	5	0	21	0.000000
17-S-81	5	0	28	0.000000

Table C.5 (continued)

Date[a] (D-M-Y)	Hour After Sunset	Number of[b] Observations of Oviposition	Observational[c] Time (min)	Weighted[d] Observations
03-S-82	5	0	11	0.000000
04-S-82	5	1	19	0.052632
10-S-82	5	0	19	0.000000
24-S-82	5	0	37	0.000000
25-S-82	5	0	18	0.000000
23-A-81	6	0	42	0.000000
13-S-81	6	0	44	0.000000
04-S-82	6	1	60	0.016667
25-S-82	6	3	60	0.050000
13-S-81	7	0	21	0.000000
04-S-82	7	0	11	0.000000
25-S-82	7	0	3	0.000000
13-S-81	8	0	39	0.000000
25-S-81	8	0	33	0.000000
13-S-81	9	0	60	0.000000
24-A-82	9	0	32	0.000000
28-A-82	9	0	27	0.000000
31-A-82	9	0	24	0.000000
04-S-82	9	0	19	0.000000
07-S-82	9	0	1	0.000000
11-S-82	9	0	11	0.000000
14-S-82	9	0	7	0.000000
18-S-82	9	0	2	0.000000
25-S-82	9	0	52	0.000000
21-A-81	10	0	20	0.000000
25-A-81	10	0	16	0.000000
28-A-81	10	0	13	0.000000
01-S-81	10	0	8	0.000000

Table C.5 (continued)

Date[a] (D-M-Y)	Hour After Sunset	Number of[b] Observations of Oviposition	Observational[c] Time (min)	Weighted[d] Observations
04-S-81	10	0	4	0.000000
13-S-81	10	0	60	0.000000
24-A-82	10	2	60	0.033333
28-A-82	10	3	53	0.056604
31-A-82	10	2	60	0.033333
04-S-82	10	0	51	0.000000
07-S-82	10	0	59	0.000000
11-S-82	10	0	59	0.000000
14-S-82	10	0	60	0.000000
18-S-82	10	0	60	0.000000
21-S-82	10	0	58	0.000000
25-S-82	10	0	53	0.000000
21-A-81	11	0	56	0.000000
25-A-81	11	0	60	0.000000
28-A-81	11	0	60	0.000000
01-S-81	11	0	60	0.000000
04-S-81	11	0	60	0.000000
08-S-81	11	0	60	0.000000
13-S-81	11	0	6	0.000000
15-S-81	11	0	51	0.000000
11-A-82	11	0	28	0.000000
31-A-82	11	0	36	0.000000
14-S-82	11	0	8	0.000000
18-S-82	11	0	23	0.000000
21-S-82	11	0	17	0.000000
25-S-82	11	0	32	0.000000
25-A-81	12	0	2	0.000000
28-A-81	12	0	7	0.000000

Table C.5 (continued)

Date[a] (D-M-Y)	Hour After Sunset	Number of[b] Observations of Oviposition	Observational[c] Time (min)	Weighted[d] Observations
01-S-81	12	0	14	0.000000
04-S-81	12	0	19	0.000000
08-S-81	12	0	25	0.000000
15-S-81	12	0	38	0.000000

[a]D-M-Y = Day, Month, Year; A = August, S = September; 81 = 1981, 82 = 1982.

[b]Total number of observations of oviposition was 121.

[c]Total number of observational minutes was 4417.

[d]Weighted Observations = $\frac{\text{Number of Observations}}{\text{Observational Time}}$

Table C.6. Sample mean and standard error of weighted observations of oviposition by female velvetbean caterpillar grouped by post-sunset hour, along with the percent normalized sample mean and standard error. Observations were made from 1980-82 at the Green Acres Research Farm, Alachua County, FL, in a 1 ha soybean field.

Hour After Sunset	n[a]	Sample Mean of the Weighted Observations (± SE)	Percent[b] Normalized Sample Mean (± SE)
1	14	.0580 ± .0181	29.35 ± 9.15
2	14	.0489 ± .0138	24.72 ± 7.00
3	12	.0301 ± .0151	15.20 ± 7.65
4	10	.0306 ± .0150	15.45 ± 7.60
5	9	.0058 ± .0058	2.96 ± 2.96
6	4	.0167 ± .0118	8.43 ± 5.96
7	3	.0000 ± .0000	.00 ± .00
8	2	.0000 ± .0000	.00 ± .00
9	10	.0000 ± .0000	.00 ± .00
10	16	.0077 ± .0043	3.90 ± 2.18
11	14	.0000 ± .0000	.00 ± .00
12	6	.0000 ± .0000	.00 ± .00

[a] n = number of weighted observations per sample mean; n is not the number of ovipositional observations. See Table C.5 for a complete listing of all observation and observational times.

[b] Percent normalized sample mean = (sample mean of the weighted observations/0.197760)*100. Percent normalized standard error = (standard error of the sampled mean/ 0.197760)*100.

Table C.7. Total oviposition per female at four different temperatures. Datum at 11.9°C is from field observation at Green Acres Research Farm, Alachua County, FL. Data of 21.1, 23.9, and 26.7°C are from Moscardi et al. (1981b) and were stored on computer cards at the time of this analysis in Building 175, Insect Population Dynamics Laboratory, University of Florida, Alachua County, Gainesville, FL.

Female Number	Total Oviposition/Female/Temperature(°C)			
	11.9	21.1	23.9	26.7
1	0	448	1508	728
2		520	912	1256
3		428	412	1384
4		600	392	608
5		640	324	296
6		372	940	620
7		296	352	1696
8		348	268	664
9		612	540	604
10		472	1744	608
11		228	284	1872
12		796	440	672
13		744	548	596
14		364	1448	584
15		176	348	1080
16		732	748	936
17		660	460	648
18		468	1504	784
19		236	444	1360
20			484	356
21			584	572
22			1976	912
23			388	1804
24			528	384
25			560	512
26			1644	
27			324	
28			644	
29			488	

Table C.8. Observational data on feeding of adult velvetbean caterpillar in a soybean field at Green Acres Research Farm, Alachua County, FL, 1980-82. Weighted observations are also given.

Date[a] (D-M-Y)	Hour[b]	Male[c] Agg	Male[d] OAgg	Male[e] All	Female[f]	Adult[g]	MFA[h] Agg	MFA[i] OAgg	Time[j]	Weight[k] 1	Weight[l] 2	Weight[m] 3	Weight[n] 4	Weight[o] 5	Weight[p] 6	Weight[q] 7
05-A-80	1	0	0	0	0	1	1	1	49	0.000000	0.000000	0.000000	0.000000	0.020408	0.020408	0.020408
01-A-81	1	0	1	1	1	0	2	2	60	0.000000	0.016667	0.016667	0.016667	0.000000	0.033333	0.033333
05-A-81	1	0	0	0	0	0	0	0	56	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
12-A-81	1	0	0	0	0	0	0	0	45	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
15-A-81	1	0	1	1	1	1	3	3	60	0.000000	0.016667	0.016667	0.016667	0.016667	0.050000	0.050000
19-A-81	1	0	1	1	0	2	3	3	60	0.000000	0.016667	0.016667	0.000000	0.033333	0.050000	0.050000
22-A-81	1	0	0	0	1	0	1	1	60	0.000000	0.000000	0.000000	0.016667	0.000000	0.016667	0.016667
26-A-81	1	0	0	0	0	0	0	0	60	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
29-A-81	1	0	0	0	0	0	0	0	35	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
02-S-81	1	0	1	1	0	0	1	1	60	0.000000	0.016667	0.016667	0.000000	0.000000	0.016667	0.016667
05-S-81	1	0	2	2	0	4	6	6	59	0.000000	0.033898	0.033898	0.000000	0.067797	0.101695	0.101695
09-S-81	1	0	0	0	0	0	0	0	49	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
12-S-81	1	0	0	0	0	0	0	0	60	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
17-S-81	1	12	0	12	0	0	12	0	60	0.200000	0.000000	0.200000	0.000000	0.000000	0.200000	0.000000
19-S-81	1	0	1	1	0	0	1	1	50	0.000000	0.020000	0.020000	0.000000	0.000000	0.020000	0.020000
24-S-81	1	0	0	0	0	0	0	0	60	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
26-A-82	1	0	0	0	0	0	0	0	40	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000

Table C.8 (continued)

Date[a] (D-M-Y)	Hour[b]	Male[c] Agg	Male[d] OAgg	Male[e] All	Female[f]	Adult[g]	MFA[h] Agg	MFA[i] OAgg	Time[j]	Weight[k] 1	Weight[l] 2	Weight[m] 3	Weight[n] 4	Weight[o] 5	Weight[p] 6	Weight[q] 7
03-S-82	1	0	2	2	0	1	3	3	10	0.000000	0.200000	0.200000	0.000000	0.100000	0.300000	0.300000
24-S-82	1	0	4	4	0	5	9	9	60	0.000000	0.066667	0.066667	0.000000	0.083333	0.150000	0.150000
05-A-80	2	0	0	0	0	4	4	4	60	0.000000	0.000000	0.000000	0.000000	0.066667	0.066667	0.066667
01-A-81	2	0	0	0	0	0	0	0	60	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
05-A-81	2	0	0	0	0	0	0	0	15	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
12-A-81	2	0	4	4	9	0	13	13	54	0.000000	0.074074	0.074074	0.166667	0.000000	0.240741	0.240741
15-A-81	2	0	1	1	2	4	7	7	60	0.000000	0.016667	0.016667	0.033333	0.066667	0.116667	0.116667
19-A-81	2	0	0	0	0	0	0	0	39	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
22-A-81	2	0	0	0	2	0	2	2	60	0.000000	0.000000	0.000000	0.033333	0.000000	0.033333	0.033333
26-A-81	2	0	0	0	0	0	0	0	30	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
29-A-81	2	0	0	0	0	0	0	0	35	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
02-S-81	2	0	0	0	4	0	4	4	60	0.000000	0.000000	0.000000	0.066667	0.000000	0.066667	0.066667
05-S-81	2	0	0	0	0	0	0	0	3	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
09-S-81	2	0	0	0	0	0	0	0	28	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
12-S-81	2	0	0	0	0	0	0	0	21	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
17-S-81	2	22	0	22	0	0	22	0	60	0.366667	0.000000	0.366667	0.000000	0.000000	0.366667	0.000000
19-S-81	2	9	7	16	0	0	16	7	60	0.150000	0.116667	0.266667	0.000000	0.000000	0.266667	0.116667
24-S-81	2	0	0	0	0	0	0	0	60	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
26-A-82	2	0	6	6	3	0	9	9	60	0.000000	0.100000	0.100000	0.050000	0.000000	0.150000	0.150000

Table C.8 (continued)

Date[a] (D-M-Y)	Hour[b]	Male[c] Agg	Mele[d] OAgg	Male[e] All	Female[f]	Adult[g]	MFA[h] Agg	MFA[i] OAgg	Time[j]	Weight[k] 1	Weight[l] 2	Weight[m] 3	Weight[n] 4	Weight[o] 5	Weight[p] 6	Weight[q] 7
03-S-82	2	0	0	0	0	0	0	0	60	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
24-S-82	2	3	2	5	5	0	10	7	45	0.066667	0.044444	0.111111	0.111111	0.000000	0.222222	0.155556
05-A-80	3	0	0	0	0	3	3	3	60	0.000000	0.000000	0.000000	0.000000	0.050000	0.050000	0.050000
01-A-81	3	0	0	0	0	0	0	0	8	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
15-A-81	3	0	0	0	7	1	8	8	35	0.000000	0.000000	0.000000	0.200000	0.028571	0.228571	0.228571
22-A-81	3	0	1	1	0	0	1	1	32	0.000000	0.031250	0.031250	0.000000	0.000000	0.031250	0.031250
26-A-81	3	0	0	0	2	0	2	2	60	0.000000	0.000000	0.000000	0.033333	0.000000	0.033333	0.033333
29-A-81	3	0	4	4	0	0	4	4	40	0.000000	0.100000	0.100000	0.000000	0.000000	0.100000	0.100000
02-S-81	3	0	0	0	0	0	0	0	15	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
09-S-81	3	0	0	0	0	0	0	0	42	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
12-S-81	3	0	0	0	0	0	0	0	49	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
17-S-81	3	29	0	29	0	0	29	0	60	0.483333	0.000000	0.483333	0.000000	0.000000	0.483333	0.000000
19-S-81	3	5	0	5	0	0	5	0	18	0.277778	0.000000	0.277778	0.000000	0.000000	0.277778	0.000000
24-S-81	3	9	0	9	0	0	9	0	37	0.243243	0.000000	0.243243	0.000000	0.000000	0.243243	0.000000
26-A-82	3	0	1	1	0	0	1	1	18	0.000000	0.055556	0.055556	0.000000	0.000000	0.055556	0.055556
03-S-82	3	0	0	0	1	0	1	1	40	0.000000	0.000000	0.000000	0.025000	0.000000	0.025000	0.025000
10-S-82	3	0	2	2	1	0	3	3	38	0.000000	0.052632	0.052632	0.026316	0.000000	0.078947	0.078947
24-S-82	3	0	7	7	6	3	16	16	50	0.000000	0.140000	0.140000	0.120000	0.060000	0.320000	0.320000
05-A-80	4	0	0	0	0	2	2	2	11	0.000000	0.000000	0.000000	0.000000	0.181818	0.181818	0.181818

Table C.8 (continued)

Date[a] (D-M-Y)	Hour[b]	Male[c] Agg	Male[d] OAgg	Male[e] All	Female[f]	Adult[g]	MFA[h] Agg	MFA[i] OAgg	Time[j]	Weight[k] 1	Weight[l] 2	Weight[m] 3	Weight[n] 4	Weight[o] 5	Weight[p] 6	Weight[q] 7
15-A-81	4	0	3	3	2	0	5	5	50	0.000000	0.060000	0.060000	0.040000	0.000000	0.100000	0.100000
16-A-81	4	0	0	0	0	1	1	1	10	0.000000	0.000000	0.000000	0.000000	0.100000	0.100000	0.100000
22-A-81	4	0	4	4	5	1	10	10	45	0.000000	0.088889	0.088889	0.111111	0.022222	0.222222	0.222222
23-A-81	4	0	0	0	0	0	0	0	3	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
26-A-81	4	0	4	4	1	0	5	5	36	0.000000	0.111111	0.111111	0.027778	0.000000	0.138889	0.138889
29-A-81	4	0	3	3	0	0	3	3	35	0.000000	0.085714	0.085714	0.000000	0.000000	0.085714	0.085714
09-S-81	4	0	0	0	1	0	1	1	38	0.000000	0.000000	0.000000	0.026316	0.000000	0.026316	0.026316
12-S-81	4	0	3	3	1	0	4	4	60	0.000000	0.050000	0.050000	0.016667	0.000000	0.066667	0.066667
17-S-81	4	17	0	17	0	0	17	0	45	0.377778	0.000000	0.377778	0.000000	0.000000	0.377778	0.000000
03-S-82	4	0	3	3	0	0	3	3	60	0.000000	0.050000	0.050000	0.000000	0.000000	0.050000	0.050000
10-S-82	4	0	2	2	1	0	3	3	60	0.000000	0.033333	0.033333	0.016667	0.000000	0.050000	0.050000
24-S-82	4	0	0	0	5	0	5	5	60	0.000000	0.000000	0.000000	0.083333	0.000000	0.083333	0.083333
16-A-81	5	0	2	2	4	0	6	6	35	0.000000	0.057143	0.057143	0.114286	0.000000	0.171429	0.171429
23-A-81	5	0	1	1	4	1	6	6	60	0.000000	0.016667	0.016667	0.066667	0.016667	0.100000	0.100000
27-A-81	5	0	0	0	2	0	2	2	33	0.000000	0.000000	0.000000	0.060606	0.000000	0.060606	0.060606
12-S-81	5	0	0	0	0	0	0	0	21	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
17-S-81	5	18	0	18	1	0	19	1	28	0.642857	0.000000	0.642857	0.035714	0.000000	0.678571	0.035714
03-S-82	5	15	1	16	1	0	17	2	11	1.363636	0.090909	1.454545	0.090909	0.000000	1.545455	0.181818
04-S-82	5	15	0	15	0	2	17	2	19	0.789474	0.000000	0.789474	0.000000	0.105263	0.894737	0.105263

Table C.8 (continued)

Date[a] (D-M-Y)	Hour[b]	Male[c] Agg	Male[d] OAgg	Male[e] All	Female[f]	Adult[g]	MFA[h] Agg	MFA[i] OAgg	Time[j]	Weight[k] 1	Weight[l] 2	Weight[m] 3	Weight[n] 4	Weight[o] 5	Weight[p] 6	Weight[q] 7
10-S-82	5	0	0	0	0	0	0	0	19	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
24-S-82	5	0	0	0	0	0	0	0	37	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
25-S-82	5	0	0	0	2	0	2	2	18	0.000000	0.000000	0.000000	0.111111	0.000000	0.111111	0.111111
16-A-81	6	0	7	7	5	3	15	15	55	0.000000	0.127273	0.127273	0.090909	0.054545	0.272727	0.272727
23-A-81	6	0	1	1	1	0	2	2	42	0.000000	0.023810	0.023810	0.023810	0.000000	0.047619	0.047619
13-S-81	6	0	0	0	0	0	0	0	44	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
04-S-82	6	0	0	0	0	0	0	0	60	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
25-S-82	6	0	0	0	3	0	3	3	60	0.000000	0.000000	0.000000	0.050000	0.000000	0.050000	0.050000
16-A-81	7	0	0	0	0	3	3	3	30	0.000000	0.000000	0.000000	0.000000	0.100000	0.100000	0.100000
13-S-81	7	0	0	0	0	0	0	0	21	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
04-S-82	7	0	0	0	0	0	0	0	11	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
25-S-82	7	0	0	0	0	0	0	0	3	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
16-A-81	8	0	0	0	2	2	4	4	60	0.000000	0.000000	0.000000	0.033333	0.033333	0.066667	0.066667
13-S-81	8	0	2	2	3	0	5	5	39	0.000000	0.051282	0.051282	0.076923	0.000000	0.128205	0.128205
25-S-82	8	5	2	7	6	0	13	8	33	0.151515	0.060606	0.212121	0.181818	0.000000	0.393939	0.242424
16-A-81	9	0	4	4	3	1	8	8	60	0.000000	0.066667	0.066667	0.050000	0.016667	0.133333	0.133333
13-S-81	9	0	0	0	2	0	2	2	60	0.000000	0.000000	0.000000	0.033333	0.000000	0.033333	0.033333
28-A-82	9	0	1	1	1	0	2	2	27	0.000000	0.037037	0.037037	0.037037	0.000000	0.074074	0.074074
31-A-82	9	0	0	0	0	0	0	0	24	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000

Table C.8 (continued)

Date[a] (D-M-Y)	Hour[b]	Male[c] Agg	Male[d] OAgg	Mele[e] All	Female[f]	Adult[g]	MFA[h] Agg	MFA[i] OAgg	Time[j]	Weight[k] 1	Weight[l] 2	Weight[m] 3	Weight[n] 4	Weight[o] 5	Weight[p] 6	Weight[q] 7
04-S-82	9	0	0	0	0	0	0	0	19	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
07-S-82	9	0	0	0	0	0	0	0	1	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
11-S-82	9	0	0	0	0	0	0	0	11	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
14-S-82	9	0	0	0	0	0	0	0	7	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
18-S-82	9	0	0	0	0	0	0	0	2	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
25-S-82	9	0	2	2	8	0	10	10	52	0.000000	0.038462	0.038462	0.153846	0.000000	0.192308	0.192308
04-A-81	10	0	0	0	0	0	0	0	30	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
07-A-81	10	0	0	0	0	0	0	0	25	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
11-A-81	10	0	0	0	0	0	0	0	20	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
14-A-81	10	0	0	0	0	0	0	0	15	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
16-A-81	10	0	1	1	5	1	7	7	45	0.000000	0.022222	0.022222	0.111111	0.022222	0.155556	0.155556
18-A-81	10	0	0	0	0	3	3	3	23	0.000000	0.000000	0.000000	0.000000	0.130435	0.130435	0.130435
21-A-81	10	0	2	2	1	0	3	3	20	0.000000	0.100000	0.100000	0.050000	0.000000	0.150000	0.150000
25-A-81	10	0	0	0	2	0	2	2	16	0.000000	0.000000	0.000000	0.125000	0.000000	0.125000	0.125000
28-A-81	10	0	0	0	0	0	0	0	13	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
01-S-81	10	0	0	0	0	0	1	1	8	0.000000	0.000000	0.000000	0.000000	0.125000	0.125000	0.125000
04-S-81	10	0	0	0	0	0	0	0	4	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
13-S-81	10	0	0	0	0	0	0	0	60	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
28-A-82	10	0	0	0	0	0	0	0	53	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000

Table C.8 (continued)

Date[a] (D-M-Y)	Hour[b]	Male[c] Agg	Male[d] OAgg	Male[e] All	Female[f]	Adult[g]	MFA[h] Agg	MFA[i] OAgg	Time[j]	Weight[k] 1	Weight[l] 2	Weight[m] 3	Weight[n] 4	Weight[o] 5	Weight[p] 6	Weight[q] 7
31-A-82	10	0	2	2	2	0	4	4	60	0.000000	0.033333	0.033333	0.033333	0.000000	0.066667	0.066667
04-S-82	10	0	0	0	0	0	0	0	51	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
07-S-82	10	0	0	0	0	0	0	0	59	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
11-S-82	10	0	0	0	0	0	0	0	59	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
14-S-82	10	0	0	0	0	0	0	0	60	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
18-S-82	10	0	1	1	2	0	3	3	60	0.000000	0.016667	0.016667	0.033333	0.000000	0.050000	0.050000
21-S-82	10	0	0	0	0	0	0	0	58	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
25-S-82	10	0	1	1	0	0	1	1	53	0.000000	0.018868	0.018868	0.000000	0.000000	0.018868	0.018868
02-0-82	10	0	0	0	1	0	1	1	40	0.000000	0.000000	0.000000	0.025000	0.000000	0.025000	0.025000
05-0-82	10	0	1	1	0	0	1	1	31	0.000000	0.032258	0.032258	0.000000	0.000000	0.032258	0.032258
09-0-82	10	0	0	0	0	0	0	0	7	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
04-A-81	11	0	0	0	0	0	0	0	30	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
07-A-81	11	0	0	0	0	0	0	0	35	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
11-A-81	11	0	0	0	0	0	0	0	40	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
14-A-81	11	0	0	0	0	0	0	0	45	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
16-A-81	11	0	1	1	0	0	1	1	48	0.000000	0.020833	0.020833	0.000000	0.000000	0.020833	0.020833
18-A-81	11	0	0	0	0	0	0	0	51	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
21-A-81	11	0	0	0	0	0	0	0	56	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
25-A-81	11	0	0	0	0	0	0	0	60	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000

Table C.8 (continued)

Date[a] (D-M-Y)	Hour[b]	Male[c] Agg	Male[d] OAgg	Male[e] All	Female[f]	Adult[g]	MFA[h] Agg	MFA[i] OAgg	Time[j]	Weight[k] 1	Weight[l] 2	Weight[m] 3	Weight[n] 4	Weight[o] 5	Weight[p] 6	Weight[q] 7
28-A-81	11	0	0	0	0	0	0	0	60	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
01-S-81	11	0	0	0	0	0	0	0	60	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
04-S-81	11	0	0	0	0	1	1	1	60	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
08-S-81	11	0	0	0	3	0	3	3	60	0.000000	0.000000	0.000000	0.050000	0.000000	0.050000	0.050000
13-S-81	11	0	0	0	0	1	1	1	6	0.000000	0.000000	0.000000	0.000000	0.166667	0.166667	0.166667
15-S-81	11	0	2	2	1	0	3	3	51	0.000000	0.039216	0.039216	0.019608	0.000000	0.058824	0.058824
31-A-82	11	0	0	0	0	0	0	0	36	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
14-S-82	11	0	0	0	0	0	0	0	8	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
18-S-82	11	0	1	1	0	0	1	1	23	0.000000	0.043478	0.043478	0.000000	0.000000	0.043478	0.043478
21-S-82	11	0	0	0	0	0	0	0	17	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
25-S-82	11	0	1	1	0	0	1	1	32	0.000000	0.031250	0.031250	0.000000	0.000000	0.031250	0.031250
02-0-82	11	0	0	0	0	0	0	0	35	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
05-0-82	11	0	1	1	2	0	3	3	39	0.000000	0.025641	0.025641	0.051282	0.000000	0.076923	0.076923
09-0-82	11	0	1	1	0	0	1	1	58	0.000000	0.017241	0.017241	0.000000	0.000000	0.017241	0.017241
25-A-81	12	0	0	0	0	0	0	0	2	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
28-A-81	12	0	0	0	0	0	0	0	7	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
01-S-81	12	0	0	0	0	0	0	0	14	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
04-S-81	12	0	0	0	0	0	0	0	19	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000

Table C.8 (continued)

Date[a] (D-M-Y)	Hour[b]	Male[c] Agg	Male[d] OAgg	Male[e] All	Female[f]	Adult[g]	MFA[h] Agg	MFA[i] OAgg	Time[j]	Weight[k] 1	Weight[l] 2	Weight[m] 3	Weight[n] 4	Weight[o] 5	Weight[p] 6	Weight[q] 7
08-S-81	12	0	0	0	0	0	0	0	25	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
15-S-81	12	0	0	0	0	0	0	0	38	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000

[a] D-M-Y = Day, Month, Year; A = August, S = September, O = October; 80 = 1980, 81 = 1981, 82 = 1982.

[b] Hour after sunset.

[c] Male Agg = number of males feeding in aggregations. Total number of observed males was 159.

[d] Male OAgg = number of males feeding that are not in aggregations. Total number of observed males was 108.

[e] Male All = number of males feeding -- all males. Total number of observed males was 267.

[f] Female = number of females feeding. Total number of observed females was 128.

[g] Adult = number of adults feeding. Adults were not sexually identified during the observations. Total number of observed adults was 53.

[h] MFA Agg = number of males (all males), females, and adults feeding. Total number of observations was 448.

[i] MFA OAgg = number of observations of males (not in aggregations), females, and adults feeding. Total number of observations was 289.

[j] Time = total observation minutes were 5865.0.

[k] Weight 1 = (Maleagg/Minute)

Table C.8 (continued)

[l]Weight 2 = (Male OAgg/Minute)

[m]Weight 3 = (Male All/Minute)

[n]Weight 4 = (Female/Minute)

[o]Weight 5 = (Adult/Minute)

[p]Weight 6 = (MFA Agg/Minute)

[q]Weight 7 = (MFA OAgg/Minute)

Table C.9. Sample mean and standard error of weighted observations of feeding velvetbean caterpillar males (in aggregations) grouped by post-sunset hour, along with the percent normalized sample mean and standard error. Observations were made from 1980-82 at the Green Acres Research Farm, Alachua County, FL, in a 1 ha soybean field.

Hour After Sunset	n[a]	Sample Mean of the Weighted Observations (± SE)	Percent Normalized[b] Sample Mean (± SE)
1	19	.0105 ± .0105	2.27 ± 2.27
2	19	.0307 ± .0205	6.63 ± 4.42
3	16	.0628 ± .0358	13.55 ± 7.72
4	13	.0291 ± .0291	6.27 ± 6.27
5	10	.2796 ± .1533	60.37 ± 33.09
6	5	.0000 ± .0000	.00 ± .00
7	4	.0000 ± .0000	.00 ± .00
8	3	.0505 ± .0505	10.90 ± 10.90
9	10	.0000 ± .0000	.00 ± .00
10	24	.0000 ± .0000	.00 ± .00
11	22	.0000 ± .0000	.00 ± .00
12	6	.0000 ± .0000	.00 ± .00

[a]n = number of weighted observations per sample mean; n is not the number of feeding males. See Table C.8 for a complete listing of all observations and observational times.

[b]Percent normalized sample mean = (sample mean of weighted observations/0.463162)*100. Percent normalized standard error = (standard error of sample mean/0.463162)*100.

Table C.10. Sample mean and standard error of weighted observations of feeding velvetbean caterpillar males (not in aggregations) grouped by post-sunset hour, along with the percent normalized sample mean and standard error. Observations were made from 1980-82 at the Green Acres Research Farm, Alachua County, FL, in a 1 ha soybean field.

Hour After Sunset	n[a]	Sample Mean of the Weighted Observations (± SE)	Percent Normalized[b] Sample Mean (± SE)
1	19	.0204 ± .0107	9.48 ± 4.98
2	19	.0185 ± .0085	8.61 ± 3.96
3	16	.0237 ± .0107	11.03 ± 4.97
4	13	.0369 ± .0112	17.14 ± 5.22
5	10	.0165 ± .0101	7.66 ± 4.67
6	5	.0302 ± .0247	14.05 ± 11.48
7	4	.0000 ± .0000	.00 ± .00
8	3	.0373 ± .0188	17.34 ± 8.76
9	10	.0142 ± .0077	6.61 ± 3.56
10	24	.0093 ± .0045	4.43 ± 2.09
11	22	.0081 ± .0031	3.76 ± 1.43
12	6	.0000 ± .0000	.00 ± .00

[a] n = number of weighted observations per sample mean; n is not the number of feeding observations. See Table C.8 for a complete listing of all observations and observational times.

[b] Percent normalized sample mean = (sample mean of weighted observations/0.215046)*100. Percent normalized standard error = (standard error of sample mean/0.215046)*100.

Table C.11. Sample mean and standard error of weighted observations of feeding velvetbean caterpillar males (all males) grouped by post-sunset hour, along with the percent normalized sample mean and standard error. Observations were made from 1980-82 at the Green Acres Research Farm, Alachua County, FL, in a 1 ha soybean field.

Hour After Sunset	n[a]	Sample Mean of the Weighted Observations (± SE)	Percent Normalized[b] Sample Mean (± SE)
1	19	.0309 ± .0142	4.56 ± 2.09
2	19	.0492 ± .0234	7.26 ± 3.45
3	16	.0865 ± .0346	12.75 ± 5.10
4	13	.0659 ± .0281	9.72 ± 4.15
5	10	.2961 ± .1591	43.65 ± 23.46
6	5	.0302 ± .0247	4.45 ± 3.64
7	4	.0000 ± .0000	.00 ± .00
8	3	.0878 ± .0639	12.95 ± 9.42
9	10	.0142 ± .0077	2.10 ± 1.13
10	24	.0093 ± .0045	1.37 ± .64
11	22	.0081 ± .0031	1.19 ± .45
12	6	.0000 ± .0000	.00 ± .00

[a] n = number of weighted observations per sample mean; n is not the number of feeding observations. See Table C.8 for a complete listing of all observations and observational times.

[b] Percent normalized sample mean = (sample mean of weighted observations/0.678208)*100. Percent normalized standard error = (standard error of weighted observations/0.678208)*100.

Table C.12. Sample mean and standard error of weighted observations of feeding velvetbean caterpillar females grouped by post-sunset hour, along with the percent normalized sample mean and standard error. Observations were made from 1980-82 at the Green Acres Research Farm, Alachua County, FL, in a 1 ha soybean field.

Hour After Sunset	n[a]	Sample Mean of the Weighted Observations (± SE)	Percent Normalized[b] Sample Mean (± SE)
1	19	.0026 ± .0014	.87 ± .47
2	19	.0242 ± .0106	7.99 ± 3.47
3	16	.0253 ± .0139	8.32 ± 4.59
4	13	.0248 ± .0098	8.15 ± 3.22
5	10	.0480 ± .0149	15.77 ± 4.92
6	5	.0329 ± .0172	10.84 ± 5.66
7	4	.0000 ± .0000	.00 ± .00
8	3	.0974 ± .0441	32.04 ± 14.50
9	10	.0274 ± .0153	9.03 ± 5.04
10	24	.0157 ± .0070	5.18 ± 2.32
11	22	.0055 ± .0032	1.81 ± 1.07
12	6	.0000 ± .0000	.00 ± .00

[a] n = number of weighted observations per sample mean; n is not the number of feeding observations. See Table C.8 for a complete listing of all observations and observational times.

[b] Percent normalized sample mean = (sample mean of weighted observations/0.303839)*100. Percent normalized standard error = (standard error of weighted observations/0.303839)*100.

Table C.13. Sample mean and standard error of weighted observations of feeding by unsexed velvetbean caterpillar adults[a] grouped by post-sunset hour, along with the percent normalized sample mean and standard error. Observations were made from 1980-82 at the Green Acres Research Farm, Alachua County, FL, in a 1 ha soybean field.

Hour After Sunset	n[b]	Sample Mean of the Weighted Observations (± SE)	Percent Normalized[c] Sample Mean (± SE)
1	19	.0169 ± .0072	12.31 ± 5.26
2	19	.0070 ± .0048	5.10 ± 3.51
3	16	.0087 ± .0049	6.30 ± 3.55
4	13	.0234 ± .0153	17.01 ± 11.11
5	10	.0122 ± .0105	8.87 ± 7.62
6	5	.0109 ± .0109	7.93 ± 7.93
7	4	.0250 ± .0250	18.18 ± 18.18
8	3	.0111 ± .0111	8.08 ± 8.08
9	10	.0017 ± .0017	1.21 ± 1.21
10	24	.0116 ± .0074	8.41 ± 5.35
11	22	.0091 ± .0076	6.61 ± 5.51
12	6	.0000 ± .0000	.00 ± .00

[a]Unsexed adults flew out of sight before a positive sexual identification could be made.

[b]n = number of weighted observations per sample mean; n is not the number of feeding observations. See Table C.8 for complete a listing of all observations and observational times.

[c]Percent normalized sample mean=(sample mean of weighted observations/0.137529)*100. Percent normalized standard error=(standard error of weighted observations/0.137529)*100.

Table C.14. Sample mean and standard error of weighted observations of feeding by males (all), females, and unsexed velvetbean caterpillar adults[a] grouped by post-sunset hour, along with the percent normalized sample mean and standard error. Observations were made from 1980-82 at the Green Acres Research Farm, Alachua County, FL, in a 1 ha soybean field.

Hour After Sunset	n[b]	Sample Mean of the Weighted Observations (± SE)	Percent Normalized[c] Sample Mean (± SE)
1	19	.0505 ± .0189	4.51 ± 1.69
2	19	.0805 ± .0263	7.19 ± 2.35
3	16	.1204 ± .0363	10.76 ± 3.25
4	13	.1141 ± .0277	10.19 ± 2.47
5	10	.3562 ± .1645	31.81 ± 14.70
6	5	.0741 ± .0509	6.62 ± 4.54
7	4	.0250 ± .0250	2.23 ± 2.23
8	3	.1963 ± .1004	17.53 ± 8.97
9	10	.0433 ± .0218	3.87 ± 1.94
10	24	.0366 ± .0114	3.27 ± 1.02
11	22	.0227 ± .0084	2.02 ± .75
12	6	.0000 ± .0000	.00 ± .00

[a]Unsexed adults flew out of sight before a positive sexual identification could be made.

[b]n = number of weighted observations per sample mean; n is not the number of feeding observations. See Table C.8 for a complete listing of all observations and observational times.

[c]Percent normalized sample mean = (sample mean of weighted observations/1.11958)*100. Percent normalized standard error = (standard error of weighted observations/1.11958)*100.

Table C.15. Sample mean and standard error of weighted observations of feeding by males (excluding aggregations), females, and unsexed velvetbean caterpillar adults[a] grouped by post-sunset hour, along with the percent normalized sample mean and standard error. Observations were made from 1980-82 at the Green Acres Research Farm, Alachua County, FL, in a 1 ha soybean field.

Hour After Sunset	n[b]	Sample Mean of the Weighted Observations (± SE)	Percent Normalized[c] Sample Mean (± SE)
1	19	.0399 ± .0171	6.08 ± 2.61
2	19	.0498 ± .0166	7.59 ± 2.54
3	16	.0577 ± .0229	8.79 ± 3.49
4	13	.0850 ± .0183	12.95 ± 2.79
5	10	.0766A ± .0216	11.67 ± 3.30
6	5	.0741A ± .0509	11.28 ± 7.75
7	4	.0250 ± .0250	3.81 ± 3.81
8	3	.1458 ± .0515	22.21 ± 7.84
9	10	.0433 ± .0218	6.60 ± 3.31
10	24	.0366 ± .0114	5.58 ± 1.74
11	22	.0227 ± .0084	3.45 ± 1.28
12	6	.0000 ± .0000	.00 ± .00

[a]Unsexed adults flew out of sight before a positive sexual identification could be made.

[b]n = number of weighted observations per sample mean; n is not the number of feeding observations. See Table C.8 for a complete listing of all observations and observational times.

[d]Percent normalized sample mean = (sample mean of weighted observations/0.656414)*100. Percent normalized standard error = (standard error of weighted observations/0.656414)*100.

APPENDIX D

ADULT DENSITY AND PHYSICAL VARIABLE DATA, AND MATHEMATICAL DESCRIPTIONS OF PHYSICAL VARIABLES

Table D.1. Total number of females, males, and adults (male and females) caught in a blacklight trap in 1980 at the Green Acres Research Farm, Alachua County, FL. Trap did not operate on dates 203, 207, 220, 225, 232, 236, 250, 251, and 254.

Calendar Date	Julian Date	Total Number		
		Females	Males	Adults
July 4	186	0	0	0
5	187	0	0	0
6	188	0	0	0
7	189	0	0	0
8	190	1	0	1
9	191	0	0	0
10	192	0	0	0
11	193	0	0	0
12	194	2	0	2
13	195	0	0	0
14	196	0	0	0
15	197	0	0	0
16	198	0	1	1
17	199	0	1	1
18	200	0	1	1
19	201	0	0	0
20	202	0	0	0
21	203	–	–	–
22	204	1	1	2
23	205	2	0	2
24	206	0	3	3
25	207	–	–	–
26	208	0	2	2
27	209	0	1	1
28	210	0	2	2
29	211	1	2	3
30	212	1	3	4

Table D.1 (continued)

Calendar Date	Julian Date	Total Number		
		Females	Males	Adults
July 31	213	2	6	8
Aug. 1	214	0	3	3
2	215	4	1	5
3	216	4	2	6
4	217	9	2	11
5	218	16	29	45
6	219	11	37	48
7	220	-	-	-
8	221	30	30	60
9	222	13	12	25
10	223	20	19	39
11	224	7	44	51
12	225	-	-	-
13	226	38	54	92
14	227	26	14	40
15	228	13	24	37
16	229	34	55	89
17	230	24	21	45
18	231	21	41	62
19	232	-	-	-
20	233	36	51	87
21	234	43	96	139
22	235	24	48	72
23	236	-	-	-
24	237	49	66	115
25	238	56	73	129
26	239	30	90	120
27	240	89	177	266
28	241	55	39	94
29	242	97	129	226

Table D.1 (continued)

Calendar Date	Julian Date	Total Number		
		Females	Males	Adults
Aug. 30	243	104	63	167
31	244	157	82	239
Sept. 1	245	179	96	275
2	246	102	36	138
3	247	111	76	187
4	248	51	29	80
5	249	62	17	79
6	250	-	-	-
7	251	-	-	-
8	252	30	11	41
9	253	24	14	38
10	254	-	-	-
11	255	11	10	21
12	256	28	19	47
13	257	22	23	45
14	258	56	25	81
15	259	52	37	89
16	260	42	30	72
17	261	28	9	37
18	262	47	36	83
19	263	25	30	55
20	264	44	59	103
21	265	34	30	64

Table D.2. Total, smoothed-total[a], and weighted[b] number of females, males, and adults (males and females) caught in a blacklight trap in 1981 at the Green Acres Research Farm, Alachua County, FL. Trap did not operate on date 174.

Calendar Date	Julian Date	Number of Females			Number of Males			Number of Total Adults		
		Total	Smoothed	Weighted	Total	Smoothed	Weighted	Total	Smoothed	Weighted
June 21	172	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
22	173	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
23	174	-	-	-	-	-	-	-	-	-
24	175	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
25	176	0	0.00	0.00	1	0.00	0.00	1	0.00	0.00
26	177	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
27	178	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
28	179	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
29	180	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
30	181	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
July 1	182	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
2	183	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
3	184	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
4	185	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
5	186	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
6	187	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00

Table D.2 (continued)

Calendar Date	Julian Date	Number of Females			Number of Males			Number of Total Adults		
		Total	Smoothed	Weighted	Total	Smoothed	Weighted	Total	Smoothed	Weighted
July 7	188	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
8	189	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
9	190	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
10	191	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
11	192	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
12	193	0	0.00	0.00	2	0.00	0.00	2	0.00	0.00
13	194	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
14	195	0	0.00	0.00	0	0.25	-1.00	0	0.25	-1.00
15	196	0	0.00	0.00	1	0.75	0.33	1	0.75	0.33
16	197	0	0.00	0.00	1	1.00	0.00	1	1.00	0.00
17	198	0	0.00	0.00	1	0.75	0.33	1	0.75	0.33
18	199	0	0.00	0.00	0	0.25	-1.00	0	0.25	-1.00
19	200	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
20	201	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
21	202	0	0.00	0.00	0	0.00	0.00	0	0.25	-1.00
22	203	1	0.00	0.00	0	0.50	-1.00	1	1.00	0.00
23	204	0	0.00	0.00	2	1.50	0.33	2	1.75	0.14
24	205	1	0.00	0.00	2	2.00	0.00	3	2.00	0.50

Table D.2 (continued)

Calendar Date	Julian Date	Number of Females			Number of Males			Number of Total Adults		
		Total	Smoothed	Weighted	Total	Smoothed	Weighted	Total	Smoothed	Weighted
July 25	206	0	0.00	0.00	2	2.00	0.00	2	2.00	0.00
26	207	0	0.00	0.00	1	2.00	-0.50	1	2.00	-0.50
27	208	1	0.00	0.00	1	2.00	-0.50	2	2.00	0.00
28	209	1	0.00	0.00	3	2.00	0.50	4	2.00	1.00
29	210	0	0.00	0.00	2	2.00	0.00	2	2.00	0.00
30	211	0	0.00	0.00	3	2.00	0.50	3	2.00	0.50
31	212	0	0.00	0.00	1	1.81	-0.45	1	1.75	-0.43
Aug. 1	213	1	0.00	0.00	2	1.44	0.39	3	1.25	1.40
2	214	0	0.00	0.00	0	1.25	-1.00	0	1.00	-1.00
3	215	0	0.25	-1.00	2	2.19	-0.09	2	2.25	-0.11
4	216	1	0.75	0.33	5	4.94	0.01	6	5.75	0.04
5	217	1	1.25	-0.20	13	7.63	0.70	14	9.00	0.56
6	218	2	1.75	0.14	8	7.94	0.01	10	9.50	0.05
7	219	2	2.00	0.00	6	6.44	-0.07	8	8.25	-0.03
8	220	2	2.00	0.00	5	4.63	0.08	7	7.00	0.00
9	221	3	2.00	0.50	3	3.00	0.00	6	5.63	0.07
10	222	2	2.00	0.00	2	1.75	0.14	4	3.63	0.10
11	223	0	2.19	-1.00	0	1.50	-1.00	0	2.00	-1.00

Table D.2 (continued)

Calendar Date	Julian Date	Number of Females			Number of Males			Number of Total Adults		
		Total	Smoothed	Weighted	Total	Smoothed	Weighted	Total	Smoothed	Weighted
Aug. 12	224	0	2.56	-1.00	4	4.00	0.00	4	4.00	0.00
13	225	4	2.75	0.45	15	9.06	0.66	19	10.50	0.81
14	226	3	3.13	-0.04	11	13.19	-0.17	14	16.25	-0.14
15	227	4	3.88	0.03	16	16.00	0.00	20	20.31	-0.02
16	228	1	5.00	-0.80	26	21.00	0.24	27	25.38	0.06
17	229	7	7.00	0.00	21	26.75	-0.22	28	29.31	-0.04
18	230	9	8.75	0.03	50	29.00	0.72	59	31.00	0.90
19	231	15	9.00	0.67	29	29.00	0.00	44	31.38	0.40
20	232	8	7.81	0.02	9	28.25	-0.68	17	31.13	-0.45
21	233	6	6.19	-0.03	24	26.75	-0.10	30	31.00	-0.03
22	234	5	5.50	-0.09	26	26.00	0.00	31	31.00	0.00
23	235	12	5.50	1.18	39	26.00	0.50	51	31.00	0.65
24	236	4	5.88	-0.32	23	24.69	-0.07	27	29.75	-0.09
25	237	10	6.63	0.51	42	22.06	0.90	52	27.25	0.91
26	238	3	7.00	-0.57	5	19.19	-0.74	8	25.00	-0.68
27	239	7	7.00	0.00	16	16.06	-0.00	23	23.00	0.00
28	240	14	7.25	0.93	42	14.25	1.95	56	22.00	1.55
29	241	22	7.50	1.93	59	13.75	3.29	81	22.00	2.68

Table D.2 (continued)

Calendar Date	Julian Date	Number of Females			Number of Males			Number of Total Adults		
		Total	Smoothed	Weighted	Total	Smoothed	Weighted	Total	Smoothed	Weighted
Aug. 30	242	8	8.75	-0.09	9	13.50	-0.33	17	23.00	-0.26
31	243	3	11.50	-0.74	1	13.38	-0.93	4	27.75	-0.86
Sept. 1	244	14	14.25	-0.02	23	13.13	0.75	37	34.25	0.08
2	245	21	16.75	0.25	39	12.19	2.20	60	34.19	0.76
3	246	18	18.00	0.00	9	10.56	-0.15	27	28.56	-0.05
4	247	11	18.00	-0.39	3	9.75	-0.69	14	25.75	-0.46
5	248	18	18.00	0.00	14	9.75	0.44	32	25.75	0.24
6	249	21	18.00	0.17	13	9.75	0.33	34	25.00	0.36
7	250	6	18.00	-0.67	3	10.50	-0.71	9	24.75	-0.64
8	251	10	18.19	-0.45	16	16.00	0.00	26	30.50	-0.15
9	252	16	18.56	-0.14	32	32.25	-0.01	48	48.00	0.00
10	253	20	18.75	0.07	68	53.19	0.28	88	70.25	0.25
11	254	18	19.06	-0.06	62	74.00	-0.16	80	90.44	-0.11
12	255	37	21.94	0.69	195	95.31	1.05	232	113.31	1.05
13	256	14	26.75	-0.48	102	105.75	-0.04	116	130.25	-0.11
14	257	30	29.00	0.03	175	106.25	0.65	205	134.50	0.52
15	258	29	29.00	0.00	104	104.00	0.00	133	133.00	0.00
16	259	23	28.25	-0.19	83	95.38	-0.13	106	123.94	-0.14

Table D.2 (continued)

Calendar Date	Julian Date	Number of Females			Number of Males			Number of Total Adults		
		Total	Smoothed	Weighted	Total	Smoothed	Weighted	Total	Smoothed	Weighted
Sept. 17	260	32	26.75	0.20	95	80.63	0.18	127	106.81	0.19
18	261	26	26.00	0.00	66	66.00	0.00	92	92.00	0.00
19	262	6	26.25	-0.77	13	53.00	-0.75	19	82.25	-0.77
20	263	1	26.75	-0.96	9	41.13	-0.78	10	75.00	-0.87
21	264	27	27.00	0.00	58	35.63	0.63	85	72.25	0.18
22	265	66	29.00	1.28	93	35.25	1.64	159	75.69	1.10
23	266	27	33.00	-0.18	37	37.94	-0.02	64	82.56	-0.22
24	267	35	35.00	0.00	39	43.31	-0.10	74	86.00	-0.14
25	268	46	35.00	0.31	46	46.00	0.00	92	85.50	0.08
26	269	48	36.00	0.33	114	46.63	1.45	162	84.50	0.92
27	270	33	38.00	-0.13	50	47.88	0.04	83	83.00	0.00
28	271	32	39.00	-0.18	47	47.00	0.00	79	78.69	0.00
29	272	42	39.00	0.08	29	41.88	-0.31	71	72.81	-0.02
30	273	39	39.00	0.00	31	35.13	-0.12	70	70.00	0.00
Oct. 1	274	29	38.75	-0.25	36	31.50	0.14	65	69.56	-0.07
2	275	41	38.25	0.07	42	32.50	0.29	83	69.19	0.20
3	276	38	37.19	0.02	31	35.50	-0.13	69	69.00	0.00
4	277	35	35.25	-0.01	26	37.50	-0.31	61	69.50	-0.12

Table D.2 (continued)

Calendar Date	Julian Date	Number of Females			Number of Males			Number of Total Adults		
		Total	Smoothed	Weighted	Total	Smoothed	Weighted	Total	Smoothed	Weighted
Oct. 5	278	34	33.81	0.01	41	38.00	0.08	75	70.50	0.06
6	279	33	33.50	-0.01	38	38.00	0.00	71	71.00	0.00
7	280	23	33.25	-0.31	18	37.50	-0.52	41	71.00	-0.42
8	281	36	32.75	0.10	49	36.50	0.34	85	71.00	0.20
9	282	35	29.38	0.19	36	33.75	0.07	71	65.00	0.09
10	283	20	20.38	-0.02	27	29.25	-0.08	47	53.00	-0.11
11	284	6	11.50	-0.48	9	23.25	-0.61	15	40.25	-0.63
12	285	9	8.25	0.09	47	15.75	1.98	56	26.75	1.09
13	286	8	8.00	0.00	12	12.00	0.00	20	20.00	0.00
14	287	1	8.00	-0.88	10	12.00	-0.17	11	20.00	-0.45
15	288	11	8.00	0.38	17	12.00	0.42	28	20.00	0.40

[a]Total numbers were smoothed with a nonlinear data-smoothing algorithm (3RSSH, twice) based on running medians (see Velleman 1980, Ryan et al. 1982).

[b]Weighted Total # = (Total # - Smoothed #)/(Smoothed #).

Table D.3. Total, smoothed-total[a], and weighted[b] number of females, males, and adults (males and females) caught in a blacklight trap in 1982 at the Green Acres Research Farm, Alachua County, FL. Trap did not operate on date 235.

Calendar Date	Julian Date	Number of Females			Number of Males			Number of Total Adults		
		Total	Smoothed	Weighted	Total	Smoothed	Weighted	Total	Smoothed	Weighted
June 21	172	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
22	173	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
23	174	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
24	175	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
25	176	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
26	177	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
27	178	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
28	179	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
29	180	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
30	181	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
July 1	182	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
2	183	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
3	184	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
4	185	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
5	186	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
6	187	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00

Table D.3 (continued)

Calendar Date	Julian Date	Number of Females			Number of Males			Number of Total Adults		
		Total	Smoothed	Weighted	Total	Smoothed	Weighted	Total	Smoothed	Weighted
July 7	188	0	0.09	-1.00	0	0.01	-1.00	0	0.07	-1.00
8	189	0	0.34	-1.00	0	0.05	-1.00	0	0.34	-1.00
9	190	1	0.59	0.70	0	0.30	-1.00	1	0.84	0.20
10	191	1	0.67	0.49	1	0.70	0.44	2	1.38	0.45
11	192	0	0.59	-1.00	1	0.97	0.03	1	1.69	-0.41
12	193	2	0.34	4.89	1	1.08	-0.07	3	1.69	0.77
13	194	0	0.09	-1.00	2	1.17	0.71	2	1.57	0.27
14	195	0	0.00	0.00	1	1.31	-0.24	1	1.52	-0.34
15	196	0	0.00	0.00	1	1.41	-0.29	1	1.51	-0.34
16	197	0	0.00	0.00	2	1.42	0.41	2	1.43	0.40
17	198	1	0.08	11.20	2	1.26	0.59	3	1.24	1.42
18	199	0	0.41	-1.00	0	0.87	-1.00	0	1.12	-1.00
19	200	0	0.95	-1.00	0	0.50	-1.00	0	1.22	-1.00
20	201	4	1.38	1.90	1	0.30	2.37	5	1.58	2.16
21	202	2	1.50	0.33	0	0.21	-1.00	2	1.93	0.03
22	203	1	1.45	-0.31	2	0.32	5.24	3	2.06	0.45
23	204	2	1.38	0.45	0	0.75	-1.00	2	2.09	-0.04
24	205	1	1.32	-0.24	1	1.44	-0.31	2	2.30	-0.13

Table D.3 (continued)

Calendar Date	Julian Date	Number of Females			Number of Males			Number of Total Adults		
		Total	Smoothed	Weighted	Total	Smoothed	Weighted	Total	Smoothed	Weighted
July 25	206	0	1.50	-1.00	3	2.29	0.31	3	3.21	-0.06
26	207	2	2.44	-0.18	3	3.28	-0.08	5	5.38	-0.07
27	208	4	3.76	0.06	4	4.14	-0.03	8	8.00	0.00
28	209	6	4.33	0.39	5	4.81	0.04	11	9.42	0.17
29	210	5	3.85	0.30	7	5.50	0.27	12	9.52	0.26
30	211	2	2.90	-0.31	2	6.08	-0.67	4	9.09	-0.56
31	212	0	2.42	-1.00	9	6.36	0.42	9	8.71	0.03
Aug. 1	213	2	2.56	-0.22	5	6.50	-0.23	7	8.66	-0.19
2	214	6	2.83	1.12	8	6.66	0.20	14	8.78	0.59
3	215	4	3.22	0.24	5	6.99	-0.28	9	9.22	-0.02
4	216	1	3.36	-0.70	9	7.20	0.25	10	9.55	0.05
5	217	10	3.02	2.32	33	7.43	3.44	43	9.78	3.40
6	218	2	3.41	-0.41	5	8.60	-0.42	7	11.86	-0.41
7	219	3	5.70	-0.47	5	13.62	-0.63	8	19.67	-0.59
8	220	10	9.73	0.03	18	25.89	-0.30	28	36.29	-0.23
9	221	16	13.28	0.20	57	38.74	0.47	73	52.67	0.39
10	222	21	14.47	0.45	57	43.41	0.31	78	58.42	0.34
11	223	15	13.93	0.08	39	37.82	0.03	54	52.28	0.03

Table D.3 (continued)

Calendar Date	Julian Date	Number of Females			Number of Males			Number of Total Adults		
		Total	Smoothed	Weighted	Total	Smoothed	Weighted	Total	Smoothed	Weighted
Aug. 12	224	10	12.84	-0.22	18	26.65	-0.32	28	40.00	-0.30
13	225	11	12.55	-0.12	18	21.06	-0.15	29	33.86	-0.14
14	226	15	14.85	0.01	23	25.11	-0.08	38	39.79	-0.05
15	227	20	20.99	-0.05	34	39.27	-0.13	54	59.90	-0.10
16	228	31	30.26	0.02	62	55.44	0.12	93	85.28	0.09
17	229	51	38.35	0.33	70	61.50	0.14	121	99.46	0.21
18	230	37	41.25	-0.10	63	60.85	0.04	100	102.42	-0.02
19	231	48	39.50	0.22	72	51.98	0.39	120	91.97	0.30
20	232	37	33.88	0.09	22	33.57	-0.34	59	66.49	-0.11
21	233	24	27.33	-0.12	11	20.75	-0.47	35	46.34	-0.24
22	234	19	24.09	-0.21	21	18.27	0.15	40	41.29	-0.03
23	235	-	-	-	-	-	-	-	-	-
24	236	28	23.52	0.19	22	18.69	0.18	50	42.88	0.17
25	237	26	25.34	0.03	16	19.31	-0.17	42	45.56	-0.08
26	238	19	31.93	-0.40	18	22.56	-0.20	37	55.84	-0.34
27	239	75	45.11	0.66	86	33.36	1.58	161	78.48	1.05
28	240	43	60.29	-0.29	38	51.72	-0.27	81	109.05	-0.26
29	241	64	71.98	-0.11	34	70.21	-0.52	98	137.84	-0.29

Table D.3 (continued)

Calendar Date	Julian Date	Number of Females			Number of Males			Number of Total Adults		
		Total	Smoothed	Weighted	Total	Smoothed	Weighted	Total	Smoothed	Weighted
Aug. 30	242	106	79.25	0.34	121	82.76	0.46	227	157.30	0.44
31	243	75	81.64	-0.08	88	86.57	0.02	163	163.42	0.00
Sept. 1	244	97	80.69	0.20	97	84.07	0.15	194	161.28	0.20
2	245	75	77.10	-0.03	75	77.73	-0.04	150	153.59	-0.02
3	246	75	69.58	0.08	68	69.65	-0.02	143	139.95	0.02
4	247	50	61.20	-0.18	59	64.05	-0.08	109	125.47	-0.13
5	248	53	56.57	-0.06	63	60.91	0.03	116	115.58	0.00
6	249	62	55.58	0.12	63	58.59	0.08	125	112.38	0.11
7	250	41	56.21	-0.27	53	57.84	-0.08	94	114.18	-0.18
8	251	72	59.86	0.20	35	57.63	-0.39	107	118.57	-0.10
9	252	52	65.23	-0.20	84	55.13	0.52	136	121.94	0.12
10	253	141	67.59	1.09	62	49.71	0.25	203	120.72	0.68
11	254	81	64.89	0.25	37	41.19	-0.10	118	110.27	0.07
12	255	43	57.60	-0.25	28	32.55	-0.14	71	92.67	-0.23
13	256	33	50.52	-0.35	27	27.78	-0.03	60	78.53	-0.24
14	257	57	46.99	0.21	50	26.28	0.90	107	71.16	0.50
15	258	51	44.82	0.14	24	26.39	-0.09	75	67.72	0.11
16	259	39	41.67	-0.06	27	26.52	0.02	66	64.53	0.02

Table D.3 (continued)

Calendar Date	Julian Date	Number of Females			Number of Males			Number of Total Adults		
		Total	Smoothed	Weighted	Total	Smoothed	Weighted	Total	Smoothed	Weighted
Sept. 17	260	31	37.29	-0.17	28	26.08	0.07	59	60.47	-0.02
18	261	39	32.69	0.19	14	25.45	-0.45	53	56.59	-0.06
19	262	29	29.00	0.00	35	24.89	0.41	64	53.09	0.21
20	263	24	26.82	-0.11	19	24.19	-0.21	43	50.58	-0.15
21	264	27	25.26	0.07	23	23.36	-0.02	50	48.33	0.03
22	265	28	23.87	0.17	37	23.14	0.60	65	46.22	0.41
23	266	15	23.46	-0.36	5	23.25	-0.78	20	45.53	-0.56
24	267	13	23.71	-0.45	9	23.25	-0.61	22	45.78	-0.52
25	268	38	23.84	0.59	38	23.25	0.63	76	45.91	0.66
26	269	46	24.06	0.91	42	23.36	0.80	88	46.98	0.87
27	270	3	24.50	-0.88	7	23.78	-0.71	10	49.13	-0.80
28	271	10	27.84	-0.64	12	25.14	-0.52	22	54.42	-0.60
29	272	35	34.38	0.02	23	28.38	-0.19	58	64.03	-0.09
30	273	57	38.09	0.50	82	31.84	1.58	139	70.60	0.97
Oct. 1	274	60	37.88	0.58	53	33.14	0.60	113	71.72	0.58
2	275	23	34.56	-0.33	24	30.04	-0.20	47	64.98	-0.28
3	276	23	29.06	-0.21	20	23.27	-0.14	43	51.33	-0.16
4	277	26	25.82	0.01	15	18.11	-0.17	41	42.93	-0.04

Table D.3 (continued)

Calendar Date	Julian Date	Number of Females			Number of Males			Number of Total Adults		
		Total	Smoothed	Weighted	Total	Smoothed	Weighted	Total	Smoothed	Weighted
Oct. 5	278	43	24.42	0.76	36	15.40	1.33	79	39.29	1.01
6	279	24	20.93	0.15	14	13.86	0.01	38	34.31	0.11
7	280	13	16.29	-0.20	14	13.11	0.07	27	29.69	-0.09
8	281	12	14.22	-0.16	15	12.08	0.24	27	27.50	-0.02
9	282	14	14.24	-0.02	5	11.22	-0.55	19	27.41	-0.31
10	283	20	15.22	0.31	9	11.16	-0.19	29	28.22	0.03
11	284	16	17.14	-0.07	14	11.67	0.20	30	29.34	0.02
12	285	17	18.66	-0.09	12	12.09	-0.01	29	30.07	-0.04
13	286	54	19.44	1.78	22	11.70	0.88	76	30.25	1.51
14	287	18	19.34	-0.07	11	9.38	0.17	29	28.74	0.01
15	288	26	15.43	0.69	5	6.09	-0.18	31	22.35	0.39
16	289	4	8.66	-0.54	1	4.52	-0.78	5	14.10	-0.65
17	290	3	5.38	-0.44	3	4.65	-0.35	6	10.73	-0.44
18	291	7	5.76	0.21	9	5.16	0.74	16	11.75	0.36
19	292	2	8.01	-0.75	7	5.52	0.27	9	14.77	-0.39
20	293	15	11.28	0.33	5	5.73	-0.13	20	17.82	0.12
21	294	18	12.88	0.40	4	5.83	-0.31	22	18.94	0.16
22	295	13	13.00	0.00	6	5.83	0.03	19	19.00	0.00

Table D.3 (continued)

[a]Total numbers were smoothed with a nonlinear data-smoothing algorithm (3RSSH, twice) based on running medians (see Velleman 1980, Ryan et al. 1982).

[b]Weighted Total # = (Total # - Smoothed #)/(Smoothed #).

Table D.4. Total females, males, and adults (females and males) caught in an adult trap-cage during 1982 at the Green Acres Research Farm, Alachua County, FL (n = 6, N = 416.59).

Julian Date	Sample Number	Total Number Females	Total Number Males	Total Number Adults	Julian Date	Sample Number	Total Number Females	Total Number Males	Total Number Adults
196	1	0	0	0	217	1	0	0	0
	2	0	0	0		2	1	0	1
	3	0	0	0		3	2	0	2
	4	0	0	0		4	2	0	2
	5	0	0	0		5	0	0	0
	6	0	0	0		6	1	0	1
203	1	0	0	0	224	1	0	0	0
	2	0	0	0		2	1	0	1
	3	0	0	0		3	1	0	1
	4	0	0	0		4	2	0	2
	5	0	0	0		5	1	0	1
	6	0	0	0		6	0	0	0
210	1	0	0	0	231	1	1	1	2
	2	0	0	0		2	0	0	0
	3	0	0	0		3	0	3	3
	4	0	0	0		4	1	0	1
	5	0	0	0		5	3	1	4
	6	0	0	0		6	1	0	1

Table D.4 (continued)

Julian Date	Sample Number	Total Number Females	Total Number Males	Total Number Adults	Julian Date	Sample Number	Total Number Females	Total Number Males	Total Number Adults
238	1	5	3	8	259	1	0	0	0
	2	4	1	5		2	4	1	5
	3	6	5	11		3	4	0	4
	4	3	4	7		4	1	2	3
	5	6	1	7		5	1	1	2
	6	2	5	7		6	0	3	3
245	1	4	5	9	266	1	0	1	1
	2	5	4	9		2	0	1	1
	3	9	7	16		3	2	0	2
	4	7	8	15		4	2	3	5
	5	4	3	7		5	7	2	9
	6	8	11	19		6	0	0	0
252	1	3	4	7	273	1	2	0	2
	2	3	4	7		2	0	0	0
	3	5	5	10		3	0	5	5
	4	6	4	10		4	0	0	0
	5	3	6	9		5	0	0	0
	6	13	8	21		6	1	0	1

Table D.4 (continued)

Julian Date	Sample Number	Total Number			Julian Date	Sample Number	Total Number		
		Females	Males	Adults			Females	Males	Adults
280	1	0	0	0	287	1	0	0	0
	2	0	0	0		2	0	0	0
	3	0	0	0		3	0	0	0
	4	0	0	0		4	2	1	3
	5	4	1	5		5	1	0	1
	6	1	0	1		6	3	0	3

Table D.5. Mean number (±SE) of females, males, and total adults per 21.16 m^2 caught in an adult trap-cage during 1982 at the Green Acres Research Farm, Alachua County, FL ($n = 6$, $N = 416.59$).

Julian Date	Mean Number (±SE)		
	Female	Male	Adult
196	.00 ± .00	.00 ± .00	.00 ± .00
203	.00 ± .00	.00 ± .00	.00 ± .00
210	.00 ± .00	.00 ± .00	.00 ± .00
217	1.00 ± .37	.00 ± .00	1.00 ± .37
224	.83 ± .31	.00 ± .00	.83 ± .31
231	1.00 ± .45	.83 ± .48	1.83 ± .60
238	4.33 ± .67	3.17 ± .75	7.50 ± .81
245	6.17 ± .87	6.33 ± 1.20	12.50 ± 1.96
252	5.50 ± 1.57	5.17 ± .65	10.67 ± 2.14
259	1.67 ± .76	1.17 ± .48	2.83 ± .70
266	1.83 ± 1.11	1.17 ± .48	3.00 ± 1.39
273	.50 ± .34	.83 ± .83	1.33 ± .80
280	.83 ± .65	.17 ± .17	1.00 ± .82
287	1.00 ± .52	.17 ± .17	1.17 ± .60

Table D.6. Mathematical description of selected physical variables (see Table 4.1). Variable values were regressed against blacklight trap catch data. Variable values are listed in Tables D.7 and D.8.

Flight Temperature (°C)

Flight Temp. = (AT°C)*(11.9°C)

where AT = mean ambient temperature °C, based on data recorded at 1 hr intervals during scotophase,
11.9°C = flight threshold temperature (see Chapter III).

Vapor Pressure Deficit (mm Hg)

$$\text{Vapor Pressure Deficit} = (1-RH)e^{21.006534\left(\frac{5317.030}{K}\right)}$$

where RH = % Relative Humidity,
e = 2.71828,
K = degree Kelvin.

Equation modified from Merva (1975).

Moonlight Illuminence

Moonlight Illuminence = I*T*C,

where I = proportional moonlight intensity (see Gardiner 1968),
T = proportional time that moon was above the horizon during the night,
C = proportional opaque cloud coverage (0 = totally overcast, 1 = totally clear sky)(see NOAA 1981, 1982).

Wind Speed (m/s)

Wind Speed = mean wind speed, based on data recorded at 15 min intervals during scotophase.

Table D.6 (continued)

Wind Direction

Wind Direction = values that vary from 1 to 360,

where 90 = due east,
180 = due south,
270 = due west,
360 = due north.

Rainfall

Rainfall = R*T,

where R = proportional amount of rainfall, based on centimeters per rainfall per night,
T = proportional length of rainfall duration, based on hours.

Barometric Pressure (MB)

Barometric Pressure = mean barometric pressure, based on data recorded at 1 h intervals during scotophase.

Table D.7. Values of physical variables regressed against blacklight trap catch data (1981). Mathematical descriptions of physical variables are listed in Table D.6.

Calendar Date	Julian Date	Flight Temp. (°C)	Vapor Press. Deficit (mm Hg)	Moonlight Intensity	Wind Speed (m/s)	Wind Direction	Rainfall	Barometric Press. (MB)
Aug. 4	216	9.11	.407	.0000	.869	161.3	.0803	1020.93
5	217	10.42	.944	.0198	.081	148.2	.0000	1019.95
6	218	11.89	1.576	.0347	.092	124.0	.0000	1015.94
7	219	13.00	1.992	.0482	.254	155.8	.0000	1013.23
8	220	13.20	1.965	.0891	.224	138.1	.0000	1015.98
9	221	13.50	2.705	.1028	.386	166.7	.0000	1020.29
10	222	11.84	2.067	.1901	.203	154.6	.0000	1020.78
11	223	10.17	.595	.0502	.297	128.3	.0031	1018.28
12	224	10.37	1.477	.1967	.253	149.2	.0000	1017.84
13	225	11.08	1.066	.2583	.571	129.2	.0000	1018.89
14	226	10.93	2.272	.8455	.505	120.1	.0000	1017.45
15	227	11.33	2.837	.9200	.647	151.8	.0000	1014.16
16	228	12.24	3.700	.7953	.773	135.6	.0000	1010.87
17	229	12.65	2.496	.4797	1.868	123.5	.0000	1010.36
18	230	11.89	2.539	.0236	2.137	93.0	.0000	1009.13
19	231	12.54	2.388	.0388	.494	156.1	.0000	1011.93

Table D.7 (continued)

Calendar Date	Julian Date	Flight Temp. (°C)	Vapor Press. Deficit (mm Hg)	Moonlight Intensity	Wind Speed (m/s)	Wind Direction	Rainfall	Barometric Press. (MB)
Aug. 20	232	10.93	.813	.0125	.701	163.6	.0000	1013.97
21	233	10.93	.858	.0228	.710	139.4	.0000	1014.85
22	234	11.58	1.396	.0408	1.693	167.4	.0003	1017.34
23	235	12.04	2.473	.0154	.950	95.8	.0000	1017.16
24	236	10.57	1.671	.0216	.801	116.1	.0000	1017.66
25	237	7.95	1.248	.0057	.597	107.4	.0000	1016.46
26	238	10.22	.980	.0000	1.307	135.6	.0000	1015.57
27	239	10.78	.675	.0000	1.556	169.5	.0467	1016.89
28	240	10.68	.866	.0000	1.161	165.1	.0000	1018.85
29	241	10.37	.520	.0000	.300	141.4	.0057	1016.48
30	242	10.57	.426	.0000	.137	139.9	.0000	1014.74
31	243	10.52	1.251	.0026	.541	117.3	.0000	1013.60
Sept. 1	244	10.83	1.654	.0021	.328	129.5	.0000	1012.95
2	245	9.97	2.021	.0063	.207	126.5	.0000	1014.32
3	246	10.73	1.600	.0079	.101	118.5	.0000	1014.65
4	247	11.74	2.092	.0167	.259	117.9	.0000	1014.71
5	248	11.99	1.414	.0000	.651	130.7	.0000	1015.35

Table D.7 (continued)

Calendar Date	Julian Date	Flight Temp. (°C)	Vapor Press. Deficit (mm Hg)	Moonlight Intensity	Wind Speed (m/s)	Wind Direction	Rainfall	Barometric Press. (MB)
Sept. 6	249	10.73	.633	.0429	.207	115.5	.0000	1016.45
7	250	9.31	.710	.0850	.274	162.1	.0000	1014.99
8	251	10.73	1.231	.0787	.064	165.8	.0000	1012.16
9	252	10.63	1.338	.1814	.194	152.9	.0000	1012.35
10	253	9.26	.629	.1092	-	-	.0000	1016.08
11	254	10.27	2.141	.3948	.731	143.9	.0000	1018.46
12	255	8.71	1.201	.4914	.391	121.7	.0000	1017.31
13	256	9.82	2.117	.9500	.402	143.9	.0000	1015.75
14	257	.83	1.648	.9700	.137	143.2	.0000	1015.81
15	258	.0	.420	.8372	.271	154.3	.0343	1015.65
16	259	3.25	.699	.1449	.710	169.5	.0000	1016.54
17	260	-	-	.1446	.937	118.0	.0000	1017.63
18	261	-	-	.1086	.697	81.9	.0000	1020.00
19	262	-	-	.1324	.073	96.5	.0000	1018.67
20	263	-	-	.0210	.322	115.4	.0000	1017.23
21	264	8.70	1.251	.0143	.516	135.4	.0038	1016.00
22	265	7.27	1.255	.0231	.052	124.7	.0000	1016.75

Table D.7 (continued)

Calendar Date	Julian Date	Flight Temp. (°C)	Vapor Press. Deficit (mm Hg)	Moonlight Intensity	Wind Speed (m/s)	Wind Direction	Rainfall	Barometric Press. (MB)
Sept. 23	266	7.73	1.249	.0093	.450	125.9	.0000	1019.55
24	267	5.41	2.469	.0051	1.451	140.4	.0000	1022.64
25	268	8.05	2.701	.0000	1.919	132.6	.0000	1020.88
26	269	6.11	.846	.0008	-	-	.0000	1020.39
27	270	7.17	1.049	.0000	.374	105.9	.0000	1019.23
28	271	6.11	1.425	.0000	.366	107.7	.0000	1018.56
29	272	8.56	1.768	.0000	.864	139.8	.0000	1019.56
30	273	5.32	1.440	.0025	.324	129.0	.0000	1019.98
Oct. 1	274	6.29	1.973	.0033	.229	118.1	.0000	1016.20
2	275	6.62	4.281	.0066	1.100	96.7	.0000	1012.88
3	276	4.16	1.439	.0126	1.561	107.7	.0000	1017.62
4	277	8.93	2.777	.0243	.889	161.6	.0000	1020.01
5	278	6.16	2.299	.0392	.644	142.1	.0000	1020.36
6	279	5.74	1.395	.0633	.144	140.0	.0000	1015.79
7	280	10.37	3.233	.0319	.259	128.1	.0000	1011.93
8	281	8.33	2.452	.0126	1.753	153.2	.0000	1015.11
9	282	9.86	1.314	.0664	.644	131.5	.0000	1016.87

Table D.7 (continued)

Calendar Date	Julian Date	Flight Temp. (°C)	Vapor Press. Deficit (mm Hg)	Moonlight Intensity	Wind Speed (m/s)	Wind Direction	Rainfall	Barometric Press. (MB)
Oct. 10	283	9.49	1.008	.0927	.592	120.0	.0000	1016.63
11	284	6.61	1.452	.1334	2.385	104.0	.0000	1018.64
12	285	3.27	1.928	.9306	2.201	107.7	.0000	1020.12
13	286	3.44	1.649	.8004	2.553	102.9	.0000	1020.58
14	287	3.10	.794	.7866	2.551	104.6	.0000	1021.38
15	288	.00	.741	.5525	.116	93.7	.0000	1018.32

Table D.8. Values of physical variables regressed against blacklight trap catch data (1982). Mathematical descriptions of physical variables are listed in Table D.6.

Calendar Date	Julian Date	Flight Temp. (°C)	Vapor Press. Deficit (mm Hg)	Moonlight Intensity	Rainfall	Barometric Press. (MB)
July 27	208	10.98	.124	.0066	.0000	1016.95
28	209	10.73	.399	.0440	.0000	1016.69
29	210	10.37	.978	.0707	.0000	1019.76
30	211	10.73	.967	.1819	.0000	1021.74
31	212	12.04	1.197	.2598	.0000	1018.99
Aug. 1	213	11.89	2.099	.4063	.0000	1017.22
2	214	12.34	.433	.4914	.0000	1014.62
3	215	10.68	.574	.6650	.0000	1014.38
4	216	10.63	.882	.6900	.0000	1016.57
5	217	9.31	.109	.6570	.0000	1017.96
6	218	8.40	.000	.5817	.0000	1018.80
7	219	11.28	.363	.3720	.0000	1019.13
8	220	11.64	1.675	.0439	.0000	1018.94
9	221	11.08	.524	.0077	.0000	1020.16
10	222	8.91	.752	.1387	.0000	1021.05
11	223	10.47	.966	.0972	.0000	1019.39
12	224	11.53	.874	.0693	.0000	1017.11
13	225	11.79	.235	.0292	.0000	1015.84
14	226	10.17	.104	.0076	.0000	1015.25
15	227	11.94	1.910	.0079	.0000	1016.27
16	228	11.48	.338	.0029	.0000	1016.20
17	229	10.32	.403	.0003	.0000	1015.24
18	230	9.82	.000	.0000	.0000	1015.30
19	231	10.42	.000	.0000	.0000	1019.74
20	232	10.78	.425	.0000	.0000	1020.18
21	233	10.92	.000	.0005	.0000	1017.25
22	234	11.39	.059	.0036	.0000	1017.71

Table D.8 (continued)

Calendar Date	Julian Date	Flight Temp. (°C)	Vapor Press. Deficit (mm Hg)	Moonlight Intensity	Rainfall	Barometric Press. (MB)
Aug. 23	235	11.29	.122	.0054	.0000	1018.63
24	236	11.84	.266	.0207	.0000	1017.89
25	237	11.48	.000	.0139	.0000	1015.41
26	238	11.79	.022	.0000	.0000	1015.01
27	239	10.68	.000	.0297	.0000	1015.67
28	240	10.42	1.262	.0530	.0061	1016.65
29	241	11.18	1.341	.1737	.0000	1020.18
30	242	9.21	.559	.2952	.0000	1021.21
31	243	9.56	.677	.4234	.0000	1020.16
Sept. 1	244	8.76	.954	.6237	.0000	1017.54
2	245	12.14	1.204	.6175	.0000	1015.25
3	246	12.75	1.381	.7100	.0000	1014.61
4	247	11.08	1.030	.6916	.0000	1015.76
5	248	10.27	.000	.3135	.0000	1013.71
6	249	9.67	.219	.3109	.0000	1018.80
7	250	9.92	.000	.1276	.0025	1017.62
8	251	11.08	.000	.0818	.0000	1016.82
9	252	11.64	.000	.0309	.0000	1016.02
10	253	10.07	.000	.0447	.0000	1015.74
11	254	11.43	.000	.0389	.0000	1017.13
12	255	10.27	.000	.0140	.0000	1019.45
13	256	9.87	.631	.0062	.0000	1013.92
14	257	8.66	.058	.0036	.0000	1016.52
15	258	10.07	.000	.0009	.0000	1014.05
16	259	11.18	.249	.0000	.0000	1013.59
17	260	9.31	.326	.0000	.0000	1014.29
18	261	10.07	.491	.0000	.0043	1013.26
19	262	9.56	.000	.0001	.0000	1013.44
20	263	10.51	.228	.0016	.0000	1014.13

Table D.8 (continued)

Calendar Date	Julian Date	Flight Temp. (°C)	Vapor Press. Deficit (mm Hg)	Moonlight Intensity	Rainfall	Barometric Press. (MB)
Sept. 21	264	9.95	.208	.0000	.0000	1013.93
22	265	4.58	.673	.0086	.0000	1017.93
23	266	4.91	.233	.0020	.0000	1018.17
24	267	7.27	.578	.0172	.0000	1013.95
25	268	4.67	.218	.0000	.1472	1015.03
26	269	3.29	.343	.1061	.0000	1011.68
27	270	5.60	.512	.1584	.0000	1015.91
28	271	7.31	.918	.2324	.0000	1016.68
29	272	9.91	.680	.0132	.0000	1016.18
30	273	10.04	.035	.0188	.0000	1015.76
Oct. 1	274	7.68	.577	.2394	.0000	1013.74
2	275	7.41	.284	.9310	.0000	1013.17
3	276	9.58	.576	.6256	.0000	1013.71
4	277	10.51	.818	.3513	.0000	1014.42
5	278	10.55	.000	.0237	.0000	1018.45
6	279	11.06	.691	.2838	.0000	1018.89
7	280	8.38	.882	.2056	.0000	1016.83
8	281	9.77	1.600	.1276	.0000	1014.28
9	282	9.26	1.069	.0700	.0000	1013.71
10	283	11.34	1.847	.0420	.0000	1013.64
11	284	9.35	.629	.0150	.0000	1015.99
12	285	8.89	2.033	.0080	.0000	1015.65
13	286	8.53	1.088	.0014	.0000	1013.49
14	287	3.31	1.014	.0029	.0000	1014.51
15	288	0.00	.907	.0002	.0000	1014.32
16	289	0.00	.291	.0000	.0000	1016.72
17	290	3.40	1.589	.0000	.0000	1021.34
18	291	2.72	.470	.0000	.0000	1021.04
19	292	4.21	.853	.0023	.0000	1021.04

Table D.8 (continued)

Calendar Date	Julian Date	Flight Temp. (°C)	Vapor Press. Deficit (mm Hg)	Moonlight Intensity	Rainfall	Barometric Press. (MB)
Oct. 20	293	3.31	.723	.0031	.0000	1019.52
21	294	5.24	.293	.0051	.0000	1018.73
22	295	5.79	.058	.0009	.0005	-

APPENDIX E

PICTORIAL KEY OF SOME LEPIDOPTERA EGGS FOUND ON SOYBEAN

Introduction

Egg density data were required to construct a model of adult velvetbean caterpillar (VBC) oviposition in soybean (see Chapters V and VI). Accurate estimation of VBC egg density depended on proper identification of Lepidoptera eggs collected during sampling. Mis-identification of VBC eggs could have led to inflated egg density estimates. The present study was initiated to identify and describe some Lepidoptera eggs found on soybean.

Materials and Methods

From 1980-82, the development and color changes of eggs of several lepidoptera species were documented. Eggs were collected with four different techniques: (1) colony adults* were allowed to oviposit on soybean in the lab; (2) wild adults were collected from soybean and allowed to oviposit on soybean in the lab; (3) wild adults were observed to oviposit in the field; and (4) eggs were found on soybean and reared to adults** (see Table E.1). All wild adults and eggs were obtained from a 1 ha soybean field (cv. Bragg) at the University of Florida's Green Acres Research Farm, Alachua County, FL (see Appendix A for agronomic practices). All adults and eggs were maintained in the lab in Percival Growth Chambers (Model I-35LL) at 26.7° ± 1°C, > 80% RH, and 14L:10D photoperiod and in the presence of a 7.5 w nightlight (General Electric, 7.5 S/CW). Egg development and coloration were monitored with a 70X dissecting microscope at variable time intervals. All eggs were

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*Colony adults were obtained from Dr. N. C. Leppla, Research Scientist, USDA Insect Attractants, Behavior, and Basic Biology Research Laboratory, Gainesville, FL 32604.

**Eggs collected with the fourth technique were exposed to 2 ± 1°C for ca. 4-12 h after collection (see Chapter V).

Table E.1. Techniques used to collect eggs of some Lepidoptera species found on soybean from 1980-82. All eggs were laid on soybean. An "X" indicates that a particular technique was used for a species.

Species Name	Colony[a] Eggs	Wild Eggs: Oviposition in Lab[b]	Wild Eggs: Found in Field[c] (Oviposition Observed)	Wild Eggs: Found in Field[d] (Oviposition Not Observed)
Anticarsia gemmatalis Hubner	X	X	X	X
Plathypena scabra (Fabricius)			X	X
Mocis latipes (Guenee)[e]				X
Pseudoplusia includens (Walker)	X			X
Heliothis zea (Boddie)[f]	X		X	X
Heliothis virescens (Fabricius)[f]	X			X
Urbanus proteus (Linnaeus)		X		X
Strymon melinus (Hubner)[g]				X
Unknown				X

[a]Colony adults were obtained from Dr. N. C. Leppla, Research Scientist, USDA Insect Attractants, Behavior, and Basic Biology Research Laboratory, Gainesville, FL 32604.

[b]Wild adults were collected from soybean and allowed to oviposit on soybean in the lab.

[c]Wild adults were observed to oviposit in the field.

Table E.1 (continued)

[d]Eggs were found on soybean. Eclosed larvae were reared on soybean to the adult stage.

[e]*M. latipes* larvae could not be reared on soybean but were reared on sandbur, *Cenchrus* sp.

[f]Eggs of *H. zea* and *H. virescens* are not distinguishable.

[g]*S. melinus* is a stem borer.

photographed with the following Olympus equipment (except where noted): OM-2 35mm SLR Camera, Auto Bellows, Macro Lens (1:35, f = 20mm, 16 to 3.5 f stop), three Electronic Flash T32's, Control Box, Emerson Micromanipulator, and Kodachrome64 slide film (KR 135-36).

Results and Discussion

A pictorial key to egg identification by species is presented on the following pages.

<u>Anticarsia</u> <u>gemmatalis</u> Hubner

Common Name:	Velvetbean Caterpillar.
Family:	Noctuidae
Egg Development, Color-Changes and Types:	
Freshly Laid..............	Light green, green, bluish green, turquoise, or off white [Fig. E.1(A)].
Middle Aged................	Same as freshly laid but with speckles. Speckles are small, irregular in shape and reddish brown, brownish red, ochre or (rarely) off white [Fig. E.1(B)]. After speckling occurs larvae develop an eye spot (i.e., six stemmata) that is visible at the edge of the micropylar area [Fig. E.1(C), see tiny dark brown spots that form a small crescent].
Old (Pre-Eclosion).........	Light brown with a visible larval head-capsule, eyes and mandibles [Fig. E.1(D)].
Eclosed....................	Whitish [Fig. E.1(E)]. Usually the chorion was eaten by a larva.
Parasitized................	Black [Fig. E.1(F and G)].
Parasitoid Emerged.........	Black with hole in egg [Fig. E.1(H)].

Egg Shape: Top View............ Circular.

Side View........... Dome like or half a circle.

Ridge Number: $\bar{x} \pm SD = 2.81 \pm 2.3$, range 21-32, n = 22.

Ridge Morphology: Distinct, easy to count.

Micropylar Area: Flat and circular. Sometimes a series of small circles can be seen.

Spatial Occurrence: Eggs laid singly.

Similar Eggs and Differences:

M. latipes................. Large reddish brown splotches, micropylar area is larger and not as defined, egg looks circular from side view.

P. scabra.................. About half the number of ridges. Ridges protrude well above egg surface.

A.

B.

C.

Figure E.1. A. gemmatalis eggs: (A) freshly laid, (B) middle aged, (C) middle aged with eye spot, (D) old or pre-eclosion, (E) eclosed, (F) parasitized, (G) parasitized, and (H) parasitoid emerged.

D.

E.

F.

Figure E.1 (continued)

G.

H.

Figure E.1 (continued)

Plathypena scabra (Fabricius)

Common Name: Green Cloverworm.

Family: Noctuidae.

Egg Development, Color-Changes and Types:

- Freshly Laid............... Light green, off white [Fig. E.2(A)].
- Middle Aged................ Same as freshly laid but with speckles. Speckles are small, irregularly shaped and reddish brown [Fig. E.2(B)].
- Old (Pre-Eclosion)......... Light brown with a visible larval head-capsule, eyes and mandibles [Fig. E.2(C)].
- Parasitized................ Black [Fig. E.2(D and E)].
- Parasitoid Emerged......... Black with hole in side [Fig. E.2(F)].

Egg Shape: Top View........... Circular.

Side View.......... Flattened dome or half circle. Egg in Fig. E.2(E) was removed from substrate and positioned for photograph. The bottom of this egg looks circular but was flat when attached to the substrate.

Ridge Number: $\bar{x} \pm SD = 16.5 \pm 1.4$, range 14-19, n = 38.

Ridge Morphology: Protrude well above egg surface (i.e., fin like). Easy to count.

Micropylar Area: Flat, composed of concentric circles.

Spatial Occurrence: Eggs laid singly.

Similar Eggs and Differences: *A. gemmatalis* and *M. latipes* have about twice as many ridges.

A.

B.

C.

Figure E.2. P. scabra eggs: (1) freshly laid, (B) middle aged, (C) old or pre-eclosion, (D) parasitized, (E) parasitized, and (F) parasitoid emerged.

D.

E.

F.

Figure E.2 (continued)

<u>Mocis</u> <u>latipes</u> (Guenee)

Common Name: Striped Grass Looper.

Family: Noctuidae.

Egg Development, Color-Changes and Types:

Freshly Laid.............. Green, light green, bluish green [Fig. E.3(A)].

Middle Aged............... Same as freshly laid but with large reddish brown splotches. Splotches are hexagonal or undefined in shape and are brown, reddish brown, or brownish red [Fig. E.3(B and C)].

Old (Pre-Eclosion)......... Unknown.

Parasitized................ Black [Fig. E.3(D and E)].

Parasitoid Emerged......... Black (sometimes ridges look whitish) with hole in egg [Fig. E.3(F)].

Egg Shape: Top View............ Circular.

Side View........... Circular.

Ridge Number: $\bar{x} \pm SD = 32.1 \pm 1.24$, range 30-34, n = 8.

Ridge Morphology: Distinct, easy to count.

Micropylar Area: Flat, composed of small circles.

Spatial Occurrence: Eggs laid singly and in groups of two or three.

Similar Eggs and Differences:

<u>A</u>. <u>gemmatalis</u>.............. Small reddish brown speckles, smaller and more defined microphylar area, dome-like side view.

<u>P</u>. <u>scabra</u>................. Approximately half the number of ridges, ridges protrude well above egg surface.

A.

B.

C.

Figure E.3. M. latipes eggs: (A) freshly laid, (B) middle aged, (C) middle aged, (D) parasitized, (E) parasitized, and (F) parasitoid emerged.

D.

E.

F.

Figure E.3 (continued)

<u>Pseudoplusia</u> <u>includens</u> (Walker)

Common Name: Soybean Looper.

Family: Noctuidae.

Egg Development, Color-Changes and Types:

Freshly Laid.............. Off white, light green. Tends to reflect small patches of color that are iridescent or opal like [Fig. E.4(A)].

Middle Aged................ Same as freshly laid.

Old (Pre-Eclosion)......... Light brown with a visible larval head-capsule, eyes and mandibles [Fig. E.4(B)].

Parasitized................ Black [Fig. E.4(C-G)].

Parasitoid Emerging........ Black [Fig. E.4 (D-G)].

Parasitoid................. <u>Trichogramma</u> sp. [Fig. E.4(E-H)].

Egg Shape: Top View............ Circular.

Side View........... A flattened dome or half circle. Egg in Fig. E.4(D) was removed from substrate and positioned for photograph.

Ridge Number: $\bar{x} \pm SD = 34.1 \pm 2.8$, range 30-40, n = 19.

Ridge Morphology: Not distinct, very difficult to count.

Micropylar Area: Flat, very undefined, very difficult to see. Ridges appear to gradually diminish into center of micropylar area.

Spatial Occurrence:	Eggs laid singly.
Similar Eggs and Differences:	Other loopers, but none were observed.

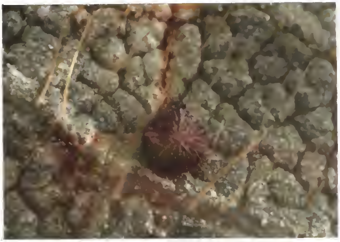
A.

B.

C.

Figure E.4. P. includens eggs: (A) freshly laid, (B) old or pre-eclosion, (C) parasitized, (D)-(G) parasitoid emerging, and (H) parasitoid.

D.



E.

F.

Figure E.4 (continued)

G.

H.

Figure E.4 (continued)

Heliothis zea (Boddie)

Common Names: Bollworm, Corn Earworm, Tomato Fruitworm.

Heliothis virescens (Fabricius)

Common Name: Tobacco Budworm.

Note: The eggs of these two species were indistinguishable.

Family: Noctuidae.

Egg Development, Color-Changes and Types:

- Freshly Laid.............. Creamy white, yellowish white, off white, whitish [Fig. E.5(A)].
- Middle Aged............... Same as freshly laid but with colored band around equator. Band is vaguely defined and reddish brown, brownish brown or brown [Fig. E.5(B)].
- Old (Pre-Eclosion)......... Creamy white with black larval head capsule.
- Parasitized............... Black [Fig. E.5(C and D)].
- Parasitoid Emerged......... Black or grayish with hole in egg [Fig. E.5(E)].

Egg Shape: Top View............ Circular.

Side View........... Barrel shaped.

Ridge Number: $\bar{x} \pm SD = 24.7 \pm 1.5$, range 21-28, n = 18.

Ridge Morphology: Distinct, easy to count.

Micropylar Area: Raised, doughnut shaped or inverted nipple. Side view shows raised micropylar area [Fig. E.5(D)].

Spatial Occurrence: Laid singly.

Similar Eggs and Differences:

U. proteus.................... Has very few ridges.

A.

B.

C.

Figure E.5. H. zea or H. virescens eggs: (A) freshly laid, (B) middle aged, (C) parasitized, (D) parasitized, and (E) parasitoid emerged.

D.

E.

Figure E.5 (continued)

Urbanus proteus (Linnaeus)

Common Names:	Bean Leafroller, Longtailed Skipper.
Family:	Hesperiidae.
Egg Development, Color-Changes and Types:	
Freshly Laid..............	Creamy white, yellowish white, off white, whitish [Fig. E.6(A and B)].
Middle Aged................	Same as freshly laid.
Old (Pre-Eclosion).........	Yellowish with black larval head capsule [Fig. E.6(C)].
Eclosed....................	Whitish [Fig. E.6(D)]. Larvae ate only the top portion of the chorion.
Parasitized................	Never observed.
Egg Shape: Top View............	Circular.
Side View...........	Barrel shaped.
Ridge Number:	$\bar{x} \pm SD = 11.6 \pm 0.7$, range 10-13, n = 46.
Ridge Morphology:	Distinct, easy to count.
Micropylar Area:	Flat, large, circular and smooth.
Spatial Occurrence:	Laid singly but usually laid in groups of two or three and attached to each other.
Similar Eggs and Differences:	
H. spp.....................	Have twice as many ridges.

A.

B.

C.

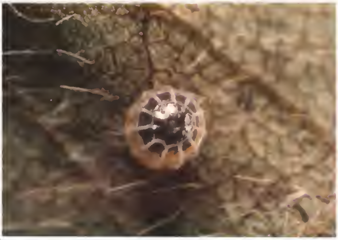


Figure E.6. U. proteus eggs: (A and B) freshly laid, (C) old or pre-eclosion, and (D) eclosed.

D.

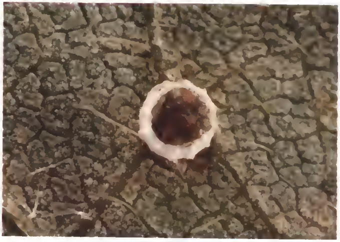


Figure E.6 (continued)

Strymon melinus (Hubner)

Common Name:	Gray Hairstreak.
Family:	Lycaenidae.
Egg Development, Color-Changes and Types:	Unknown, but observed eggs were whitish green [Fig. E.7(A)]. Eclosed eggs were whitish. Not known if chorion usually is eaten [Fig. E.7(B)].
Egg Shape: Top View............	Circular
Side View...........	Not distinct.
Ridge Number:	Not countable or observable.
Chorion Morphology:	Egg surface is covered with tiny outward projections of the chorion.
Micropylar Area:	Not distinct.
Spatial Occurrence:	Eggs laid singly.
Similar Eggs and Differences:	Other hairstreaks, but none were observed.

A.

B.

Figure E.7. S. melinus eggs: (A) unhatched and (B) eclosed.

Unknown Species

Common Name:	Unknown.
Family:	Noctuidae (?).
Egg Development, Color-Changes and Types:	
Freshly Laid..............	Whitish, grayish white, yellowish white [Fig. E.8(A)].
Middle Aged..............	Same as freshly laid but with reddish-brown band around egg and reddish-brown splotch under the microphylar area [Fig. E.8(B)].
Old (Pre-Eclosion).........	Unknown.
Parasitized................	Black [Fig. E.8(C)].
Egg Shape: Top View............	Circular.
Side View...........	Dome like.
Ridge Number:	26, n = 1.
Ridge Morphology:	Distinct, easy to count.
Micropylar Area:	Nipple like.
Spatial Occurrence:	Eggs laid singly.
Similar Eggs and Differences:	Unknown.

A.

B.

C.

Figure E.8. Eggs of unknown species: (A) freshly laid, (B) middle aged, and (C) parasitized.

Unknown Species

Common Name:	Unknown.
Family:	Noctuidae (?).
Egg Development, Color-Changes and Types:	
Parasitoid Emerged.........	Black with hole in egg [Fig. E.9(A)].
Egg Shape: Top View............	Circular.
Side View...........	Not recorded.
Ridge Number:	28, n = 1.
Ridge Morphology:	Distinct, easy to count.
Micropylar Area:	Depressed.
Spatial Occurrence:	Egg laid singly.
Similar Eggs and Differences:	Unknown.

Figure E.9. Egg of unknown species (parasitoid emerged).

APPENDIX F

EGG DENSITY DATA

Table F.1. Mean number of freshly-laid velvetbean caterpillar eggs per soybean plant (1981) found in a 1 ha soybean field[a] at the Green Acres Research Farm, Alachua County, FL.

Calendar Date	Julian Date	Sample Size[b]	Sample Unit Size[c]	Mean No. of Eggs/Plant (± SD)
June 23	173	30	1	.000 ± .000
25	176	30	1	.000 ± .000
29	180	30	1	.000 ± .000
July 6	187	30	1	.000 ± .000
9	190	30	1	.000 ± .000
12	194	30	1	.000 ± .000
16	197	30	1	.000 ± .000
20	201	30	1	.000 ± .000
23	204	30	1	.033 ± .183
27	208	70	1	.029 ± .168
30	211	70	1	.014 ± .120
Aug. 3	215	70	1	.029 ± .168
6	218	70	1	.014 ± .120
10	222	70	1	.086 ± .282
13	225	70	1	.086 ± .329
17	229	70	1	.203 ± .558
20	232	70	1	.200 ± .651
24	236	70	1	.101 ± .349
27	239	70	1	.214 ± .478
31	243	70	1	.203 ± .472
Sept. 3	246	70	1	.243 ± .494
7	250	70	1	.271 ± .658
14	257	70	1	.435 ± .630

[a]Mean number of soybean plants per 0.91 m-row was 28.267.

[b]Sample size was the number of plants sampled.

[c]Sample unit size was based on an individual soybean plant; i.e., the sample unit size was one soybean plant.

Table F.2. Mean number of freshly-laid velvetbean caterpillar eggs per soybean plant (1982) found in a 1 ha soybean field[a] at the Green Acres Research Farm, Alachua County, FL.

Calendar Date	Julian Date	Sample Size[b]	Sample Unit Size[c]	Mean No. of Eggs/Plant (± SD)
June 21	172	70	1	.000 ± .000
25	176	70	2	.000 ± .000
28	179	70	2	.000 ± .000
July 2	183	70	2	.000 ± .000
5	186	70	2	.014 ± .014
9	190	70	2	.000 ± .000
12	193	70	2	.000 ± .000
16	197	70	2	.043 ± .042
19	200	70	2	.029 ± .028
23	204	70	2	.071 ± .096
26	207	70	2	.357 ± .523
30	211	70	2	.557 ± .801
Aug. 2	214	70	2	.857 ± 1.458
6	218	70	1	.500 ± .544
9	221	70	1	.557 ± .772
13	225	50	1	.840 ± 1.239
16	228	41	1	.854 ± 1.478
20	232	30	1	1.100 ± 1.269
23	235	30	1	1.333 ± 1.709
27	239	30	1	1.400 ± 1.379
30	242	30	1	1.300 ± 1.784
Sept. 3	246	30	1	.633 ± .890
6	249	30	1	.733 ± .944
10	253	30	1	.933 ± 1.143
13	256	30	1	.800 ± 1.127
17	260	30	1	.767 ± 1.194
20	263	30	1	1.833 ± 2.718
24	267	30	1	.767 ± .898
27	270	30	1	.800 ± 1.243
Oct. 1	274	30	1	.567 ± .817
4	277	30	1	.667 ± 1.729
8	281	30	1	.067 ± .254
11	284	30	1	.133 ± .316
15	288	30	1	.000 ± .000

[a]Mean number of soybean plants per 0.91 m-row was 12.733.

[b]Sample size was the number of plants sampled.

[c]Sample unit size was based on individual soybean plants; i.e., the sample unit size varied from one to two plants.

APPENDIX G

SAS PROGRAMS AND DATA FILES FOR MODEL OF ADULT AND EGG POPULATIONS

Table G.1. SAS program of 1981 model of adult and egg populations of velvetbean caterpillar. Data file of the model is listed in Table G.2.

```
//PMODEL81 JOB (1001,2064,5,5,0),'BMG',CLASS=A,MSGLEVEL=(2,0)
/*PASSWORD
/*ROUTE  PRINT LOCAL
//EXEC SAS,REGION=800K

**********************************************************************
***                  PMODEL81 = PROGRAM, MODEL, 1981               ***
**********************************************************************;

**********************************************************************
***    IN THE INPUT STATEMENT:                                     ***
***        JULIAN = Julian date.                                   ***
***          FBLT = Total number of females captured in BLT.       ***
***          LB05 = Lower bound of 95% confidence interval, egg    ***
***                   density per .91 m-row.                       ***
***          EEGG = Estimated egg density per .91 m-row.           ***
***          UB05 = Upper bound of 95% confidence interval, egg    ***
***                   density per .91 m-row.                       ***
***           SOY = Soybean phenological stage.                    ***
**********************************************************************;

**********************************************************************
***    IN THE EQUATIONS:                                           ***
***        FTOTAL = Total number of females in the field.          ***
***            VF = Virgin females, proportion of females that     ***
***                   are not mated.                               ***
***          MORT = Mortality (proportional) of mated females      ***
***                   per day.                                     ***
***           OVI = Total number of eggs laid per female.          ***
***          TEGG = Total number of eggs laid in the field.        ***
***          PEGG = Predicted egg density per .91 m-row.  The      ***
***                   constant, 11935.696, represents the total    ***
***                   number of .91 m-row sections of soybean in   ***
***                   the field.                                   ***
**********************************************************************;

DATA BG1;
INPUT JULIAN FBLT LB05 EEGG UB05 SOY;
FTOTAL = 134.11 + 23.20*FBLT;
VF = 0;
MORT = 0;

If  1 < = SOY < =  5 THEN OVI =   0;
If  5 <   SOY < =  9 THEN OVI =  40;
If  9 <   SOY < = 14 THEN OVI = 220;
If 14 <   SOY < = 15 THEN OVI =  80;
If 15 <   SOY < = 17 THEN OVI = 210;
If 17 <   SOY < = 19 THEN OVI =  60;
If 19 <   SOY < = 20 THEN OVI =   0;
```

Table G.1 (continued)

```
TEGG = FTOTAL * (1-VF) * (1-MORT) * OVI;
PEGG = TEGG/11935.696;
CARDS;
/*INCLUDE DMODEL81.DAT
;
***********************************
***  DATA FILE IS DMODEL81.DAT  ***
***********************************;
OPTIONS NOCENTER;

PROC PRINT DATA=BG1;
    VAR JULIAN SOY FBLT FTOTAL VF MORT OVI TEGG LB05 EEGG UB05 PEGG;
    TITLE 'MODEL 1981';

PROC PLOT DATA=BG1;
    PLOT LB05*JULIAN='-'
         EEGG*JULIAN='E'
         UB05*JULIAN='-'
         PEGG*JULIAN='P'/OVERLAY;
    TITLE 'MODEL 1981';

***  THIS IS FILE PMODEL81  ***;
/*
```

Table G.2. Data set (DMODEL81.DAT) for 1981 model of adult and egg populations of velvetbean caterpillar. See the comment statements in Table G.1 for definitions of the column headings.

JULIAN	FBLT	LB05	EEGG	UB05	SOY
173	0	0.00	0.00	0.00	1
174	0	.	.	.	1
175	0	.	.	.	1
176	0	0.00	0.00	0.00	1
177	0	.	.	.	1
178	0	.	.	.	1
179	0	.	.	.	1
180	0	0.00	0.00	0.00	2
181	0	.	.	.	2
182	0	.	.	.	2
183	0	.	.	.	2
184	0	.	.	.	2
185	0	.	.	.	2
186	0	.	.	.	2
187	0	0.00	0.00	0.00	3
188	0	.	.	.	3
189	0	.	.	.	3
190	0	0.00	0.00	0.00	4
191	0	.	.	.	4
192	0	.	.	.	4
193	0	.	.	.	4
194	0	0.00	0.00	0.00	5
195	0	.	.	.	5
196	0	.	.	.	5
197	0	0.00	0.00	0.00	6
198	0	.	.	.	6
199	0	.	.	.	6
200	0	.	.	.	6
201	0	0.00	0.00	0.00	7
202	0	.	.	.	7
203	1	.	.	.	7
204	0	0.00	0.94	2.79	7
205	1	.	.	.	7
206	0	.	.	.	7
207	0	.	.	.	7
208	1	0.00	0.81	1.92	11
209	1	.	.	.	11
210	0	.	.	.	11
211	0	0.00	0.40	1.20	11
212	0	.	.	.	11
213	1	.	.	.	11
214	0	.	.	.	11

Table G.2 (continued)

JULIAN	FBLT	LB05	EEGG	UB05	SOY
215	0	0.00	0.81	1.92	11
216	1	.	.	.	11
217	1	.	.	.	11
218	2	0.00	0.40	1.20	11
219	2	.	.	.	11
220	2	.	.	.	11
221	3	.	.	.	11
222	2	0.56	2.42	4.29	12
223	0	.	.	.	12
224	0	.	.	.	12
225	4	0.24	2.42	4.60	12
226	3	.	.	.	12
227	4	.	.	.	12
228	1	.	.	.	12
229	7	2.04	5.73	9.43	12
230	9	.	.	.	12
231	15	.	.	.	12
232	8	1.35	5.65	9.96	13
233	6	.	.	.	13
234	5	.	.	.	13
235	12	.	.	.	13
236	4	0.55	2.87	5.18	14
237	10	.	.	.	14
238	3	.	.	.	14
239	7	2.89	6.06	9.23	14
240	14	.	.	.	14
241	22	.	.	.	14
242	8	.	.	.	14
243	3	2.61	5.74	8.86	15
244	14	.	.	.	15
245	21	.	.	.	15
246	18	3.59	6.87	10.14	15
247	11	.	.	.	15
248	18	.	.	.	15
249	21	.	.	.	15
250	6	3.32	7.67	12.03	15
251	10	.	.	.	15
252	16	.	.	.	15
253	20	.	.	.	15
254	18	.	.	.	15
255	37	.	.	.	15
256	14	.	.	.	15
257	30	8.12	12.29	16.46	16

Table G.3. SAS program of 1982 model of adult and egg populations of velvetbean caterpillar. To run the model without a variable oviposition rate replace the present OVI function with the phrase "OVI = 220;". Data file of the model is listed in Table G.4.

```
//PMODEL82 JOB (1001,2064,5,5,0),'BMG',CLASS=A,MSGLEVEL=(2,0)
/*PASSWORD
/*ROUTE  PRINT LOCAL
//EXEC SAS,REGION=800K

**********************************************************************
***                 PMODEL82 = PROGRAM, MODEL, 1982                ***
**********************************************************************;

**********************************************************************
***    IN THE INPUT STATEMENT:                                     ***
***        JULIAN = Julian date.                                   ***
***          FBLT = Total number of females captured in BLT.       ***
***          LB05 = Lower bound of 95% confidence interval, egg    ***
***                    density per .91 m-row.                      ***
***          EEGG = Estimated egg density per .91 m-row.           ***
***          UB05 = Upper bound of 95% confidence interval, egg    ***
***                    density per .91 m-row.                      ***
***           SOY = Soybean phenological stage.                    ***
**********************************************************************;

**********************************************************************
***    IN THE EQUATIONS:                                           ***
***        FTOTAL = Total number of females in the field.          ***
***            VF = Virgin females, proportion of females that     ***
***                    are not mated.                              ***
***          MORT = Mortality (proportional) of mated females      ***
***                    per day.                                    ***
***           OVI = Total number of eggs laid per female.          ***
***          TEGG = Total number of eggs laid in the field.        ***
***          PEGG = Predicted egg density per .91 m-row.  The      ***
***                    constant, 12469.859, represents the total   ***
***                    number of .91 m-row sections of soybean in  ***
***                    the field.                                  ***
**********************************************************************;

DATA BG1;
INPUT JULIAN FBLT LB05 EEGG UB05 SOY;
FTOTAL = 134.11 + 23.20*FBLT;
VF = 0;
MORT = 0;
```

Table G.3 (continued)

```
If  1 < = SOY < =   5 THEN OVI =   0;
If  5 <   SOY < =   9 THEN OVI =  40;
If  9 <   SOY < =  14 THEN OVI = 220;
If 14 <   SOY < =  15 THEN OVI =  80;
If 15 <   SOY < =  17 THEN OVI = 210;
If 17 <   SOY < =  19 THEN OVI =  60;
If 19 <   SOY < =  20 THEN OVI =   0;

EGG = FTOTAL * (1-VF) * (1-MORT) * OVI;
PEGG = TEGG/12469.859;
CARDS;
/*INCLUDE DMODEL82.DAT
;
***********************************
***  DATA FILE IS DMODEL82.DAT  ***
***********************************;
OPTIONS NOCENTER;

PROC PRINT DATA=BG1;
    VAR JULIAN SOY FBLT FTOTAL VF MORT OVI TEGG LB05 EEGG UB05 PEGG;
    TITLE 'MODEL 1982';

PROC PLOT DATA=BG1;
    PLOT LB05*JULIAN='-'
         EEGG*JULIAN='E'
         UB05*JULIAN='-'
         PEGG*JULIAN='P'/OVERLAY;
    TITLE 'MODEL 1982';

***  THIS IS FILE PMODEL82  ***;
/*
```

Table G.4. Data set (DMODEL82.DAT) for 1982 model of adult and egg populations of velvetbean caterpillar. See the comment statements in Table G.3 for definitions of the column headings.

JULIAN	FBLT	LB05	EEGG	UB05	SOY
172	0	0.00	0.00	0.00	1
173	0	.	.	.	1
174	0	.	.	.	1
175	0	.	.	.	1
176	0	0.00	0.00	0.00	1
177	0	.	.	.	1
178	0	.	.	.	1
179	0	0.00	0.00	0.00	2
180	0	.	.	.	2
181	0	.	.	.	2
182	0	.	.	.	2
183	0	0.00	0.00	0.00	3
184	0	.	.	.	3
185	0	.	.	.	3
186	0	0.00	0.09	0.27	4
187	0	.	.	.	4
188	0	.	.	.	4
189	0	.	.	.	4
190	1	0.00	0.00	0.00	5
191	1	.	.	.	5
192	0	.	.	.	5
193	2	0.00	0.00	0.00	5
194	0	.	.	.	5
195	0	.	.	.	5
196	0	.	.	.	5
197	0	0.00	0.27	0.58	6
198	1	.	.	.	6
199	0	.	.	.	6
200	0	0.00	0.18	0.43	7
201	4	.	.	.	7
202	2	.	.	.	7
203	1	.	.	.	7
204	2	0.00	0.45	0.92	8
205	1	.	.	.	8
206	0	.	.	.	8
207	2	1.20	2.27	3.35	10
208	4	.	.	.	10
209	6	.	.	.	10
210	5	.	.	.	10
211	2	2.21	3.55	4.88	11
212	0	.	.	.	11
213	2	.	.	.	11

Table G.4 (continued)

JULIAN	FBLT	LB05	EEGG	UB05	SOY
214	6	3.66	5.46	7.26	11
215	4	.	.	.	11
216	1	.	.	.	11
217	10	.	.	.	11
218	2	4.17	6.37	8.57	12
219	3	.	.	.	12
220	10	.	.	.	12
221	16	4.47	7.09	9.71	12
222	21	.	.	.	12
223	15	.	.	.	12
224	10	.	.	.	12
225	11	6.77	10.70	14.62	12
226	15	.	.	.	12
227	20	.	.	.	12
228	31	6.13	10.87	15.61	13
229	51	.	.	.	13
230	37	.	.	.	13
231	48	.	.	.	13
232	37	8.23	14.01	19.79	14
233	24	.	.	.	14
234	19	.	.	.	14
235	24	9.19	16.97	24.76	14
236	28	.	.	.	14
237	26	.	.	.	14
238	19	.	.	.	14
239	75	11.54	17.83	24.11	15
240	43	.	.	.	15
241	64	.	.	.	15
242	106	8.42	16.55	24.68	15
243	75	.	.	.	15
244	97	.	.	.	15
245	75	.	.	.	15
246	75	4.01	8.06	12.12	15
247	50	.	.	.	15
248	53	.	.	.	15
249	62	5.03	9.34	13.64	15
250	41	.	.	.	15
251	72	.	.	.	15
252	52	.	.	.	15
253	141	6.68	11.88	17.09	15
254	81	.	.	.	15
255	43	.	.	.	15
256	33	5.05	10.19	15.32	16
257	57	.	.	.	16
258	51	.	.	.	16

Table G.4 (continued)

JULIAN	FBLT	LB05	EEGG	UB05	SOY
259	39	.	.	.	16
260	31	4.32	9.76	15.20	16
261	39	.	.	.	16
262	29	.	.	.	16
263	24	10.96	23.34	35.72	16
264	27	.	.	.	16
265	28	.	.	.	16
266	15	.	.	.	16
267	13	5.67	9.76	13.85	17
268	38	.	.	.	17
269	46	.	.	.	17
270	3	4.52	10.19	15.85	17
271	10	.	.	.	17
272	35	.	.	.	17
273	57	.	.	.	17
274	60	3.49	7.22	10.94	18
275	23	.	.	.	18
276	23	.	.	.	18
277	26	0.61	8.49	16.37	18
278	43	.	.	.	18
279	24	.	.	.	18
280	13	.	.	.	18
281	12	0.00	0.85	2.01	18
282	14	.	.	.	18
283	20	.	.	.	18
284	16	0.26	1.70	3.14	19
285	17	.	.	.	19
286	54	.	.	.	19
287	18	.	.	.	19
288	26	0.00	0.00	0.00	20

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BIOGRAPHICAL SKETCH

A long long time ago, I was born in Charlotte, North Carolina (May 28, 1951). My wonderful parents, Ben and Nancy Gregory, bestowed upon me the immortal need to move and live in different places. So far I have lived in either 33 or 34 different places, and for someone of my youth there is no telling how many additional places I will be able to move to before my life is over. If everything falls into place my name will appear in the Guinness Book of World Records. Anyway, during one of my migratory urges in 1978, I discovered that I liked moths and butterflies, so I dashed off to the University of Florida to become an entomologist and be rich and famous. Since that time I've become a renowned entomologist and scientist, and I dare write that my reputation has reached such gigantic proportions that it is not uncommon to hear my name spoken with the likes of Darwin, Pasteur and Edison.

These past eight years in graduate school have been extremely rewarding, as I have learned everything you ever wanted to know about the velvetbean caterpillar but were afraid to ask. Believe me, there are people that are afraid to ask questions about this animal. Fortunately, a few years ago I stumbled into Snuffy's Restaurant and Bar where I have since spent many a night signing autographs, drinking Heinekens with my friends and chasing all of those gorgeous ladies that frequented the bar.

Gainesville and its memories are history, as I have moved to the cultural mecca of Louisiana, replete with crayfish and Cajuns. However,

I plan to return to Gainesville as a grey-haired alumnus at least once a year and lay a wreath on the tomb of the unknown graduate student. My typist is going to love this biographical sketch, as I hope you did.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

C. S. Barfield

C. S. Barfield, Chairman
Professor of Entomology and Nematology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

J. L. Stimac

J. L. Stimac
Associate Professor of Entomology and Nematology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Frank Slansky Jr.

Frank Slansky, Jr.
Associate Professor of Entomology and Nematology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

K J Boote

K. J. Boote
Professor of Agronomy

This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

May, 1986

Jack L. Fry

Dean, College of Agriculture

Dean, Graduate School